The effect of a temporally variable environment and grazing on lizards in mulga (*Acacia aneura*) shrublands of central Australia

by

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STATEMENT OF SOURCES

I hereby declare that the work herein, now submitted as a thesis for the degree of Doctor of Philosophy of the Northern Territory University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I hereby certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not being currently submitted in candidature for any other degree.

Christine Schlesinger

May, 1999
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ABSTRACT

The provision of artificial sources of water for domestic stock in arid Australia has resulted in high levels of grazing over extensive areas, and the impact on native fauna is likely to be widespread. However, there is little direct evidence of the effect of grazing on lizards, and particularly on the relationship between climate variability and grazing in determining the distribution and abundance of lizard assemblages. This study investigates the effect of grazing on ground-active lizards in a highly variable climate. Populations of ground-dwelling lizards were monitored at eight sites between September 1993 and December 1995. The study sites were in mulga (Acacia aneura) tall shrubland on a pastoral property in central Australia, where sites were categorised as having high and low levels of grazing based on their distance from artificial water points for cattle.

Because lizards were sampled solely by means of pitfall traps, I conducted an experiment to test the hypothesis that ground cover affects the efficiency of pitfall traps in capturing lizards. Reducing ground cover had no effect on the subsequent rates at which lizards were captured, compared with control sites, or rates of capture before grass was cut. I conclude that pitfall-trapping is a valid technique for comparing lizard populations in mulga shrublands which are subject to different levels of grazing within the range of vegetation covers used in this study.

Twenty-three species and 2249 individual lizards were captured during the study. For six frequently captured species, patterns of activity and abundance and variation in growth and body condition (a measure of mass in relation to body length) were considered in detail. The time when lizards were active in different years was variable and did not correspond closely to seasons, except for geckos. Three diurnally active species (the skinks Ctenotus leonhardii and Ctenotus schomburgkii and the agamid Ctenophorus nuchalis) delayed spring activity considerably after a long dry period in 1994, which coincided with low rates of plant growth, but after rain in early 1995 lizards maintained high levels of activity into autumn and winter. Growth rates and body condition of lizards also varied over the period of study among these species. Body condition was low in spring 1994 during the dry period. In 1995, when rainfall was higher than average, activity levels were high and body condition improved. Growth rates were also higher in 1995 when lizards were active for longer, compared with 1994, but growth rate per unit time active was comparable between the two years. In contrast to the diurnal lizards, the activity of three gecko species (Diplodactylus conspicillatus, Diplodactylus stenodactylus and Rhynchoedura ornata) was more consistently correlated with temperature, and activity was generally restricted to the
warmer months of each year. Body condition of geckos did not differ between years. Correlations between the activity of each species of lizard and environmental variables, including temperature, invertebrate biomass and plant growth, differed according to the time scale considered and when each species was active in a particular year. It appears that temporal patterns of activity are crucial in determining body condition and rate of growth of lizards at different times because they determine how effectively lizards can make use of available resources.

The agamid *Ctenophorus nuchalis* was found almost exclusively at sites that were close to artificial water points, with high levels of grazing. These sites were characterised by comparatively large areas of open ground. In contrast, the total number of skinks captured was greater at sites with low levels of grazing in nine of eleven species and the abundance of skinks as a family group was significantly higher at sites with low levels of grazing. *Ctenotus leonhardii* and *Ctenotus schomburgkii*, were generally more abundant at sites with low grazing levels, but this trend varied with time. Differences in skink abundance between sites with different grazing levels were least apparent in the year when activity was delayed.

Vegetation cover was measured twice during the study. The relative cover of ground vegetation among sites was not consistent between years, but despite this variation, the abundance of skinks was positively correlated with the cover of ground vegetation at different sites in spring 1994 and 1995. In the dry year (1994), when abundance of lizards was low, there was no significant difference in the number of skinks captured, or the cover of ground vegetation, between sites with high and low levels of grazing. In the wet year (1995) the cover of vegetation was higher at sites with low levels of grazing and the abundance of skinks was also higher at these sites. Hence, in this environment, differences in skink abundance between sites with different grazing levels appear to be related to differences in ground vegetation and are not always perceptible because the cover of vegetation is highly variable over time. The two species of *Ctenotus* also had higher body condition at sites with low levels of grazing compared to at heavily grazed sites at the end of 1995 but there were no differences in body condition with respect to grazing level in 1994. There were no significant differences in the abundance or body condition of nocturnal species between sites with different levels of grazing at any time, and the abundance of these species was not correlated with vegetation cover.

Cover from vegetation at canopy level was higher at sites with low levels of grazing, and shaded micro-habitats were more common across space and time at these sites. Shrub canopy and ground vegetation may both provide important sources of cover for diurnally active lizards when temperatures are very high, and differences in the shelter
provided by plants at sites with different levels of grazing may be significant for these species. The skinks captured in this study are widely foraging species and thus are exposed to a range of thermal micro-habitats which vary according to vegetation cover. These skinks probably also spend a considerable amount of time foraging within and around clumps of grass. Agamids, like the skinks captured in the study area, are heliothermic, diurnally active lizards, but their physiology, foraging mode and thermoregulatory behavior differ considerably from the skinks. Agamids are less likely to be adversely affected by high temperatures and some species probably benefit from large areas of open ground if suitable foraging perches are available. Ground-active geckos and pygopods, in contrast, may not be affected by grazing in mulga shrublands, because the effect of vegetation cover on the thermal environment is largely irrelevant for nocturnal species.

This study has identified clear differences between nocturnal and diurnal lizards in their response to variable rainfall and in their abundance at sites with different levels of grazing. Further work is required to determine whether these differences are consistent under other climatic sequences and in other habitats. Specific focus on the relationship between the abundance of some lizard species and the cover of vegetation is also necessary. Grazing by cattle has resulted in considerable change to habitats in the central Australian region. This study has shown that patterns in the landscape, particularly variations in ground cover, which result from concentrated grazing around artificial water points affect the distribution and abundance of some lizard species. Based on these findings I recommend that the current diversity of habitats be maintained until further information is available, and particularly that the areas which are currently remote from water be preserved.
GENERAL INTRODUCTION

In central Australia annual rainfall averages about 250 mm, but the timing and intensity of precipitation both within and between years is highly variable, and long periods without any rain are common. Temperatures during the summer months can be high, often above 40°C. These conditions, at least superficially, create an inhospitable environment for vertebrates. However, one group, the reptiles, has been particularly successful throughout the Australian desert regions, as is evident by their unusually high diversity and abundance compared with mammals or birds, or reptiles in arid environments on other continents (Pianka 1969; Morton & James 1988). Presumably the success of reptiles, at least in part, is due to the distinct advantages of ectothermy over endothermy in enabling reptiles to survive through periods of environmental stress at relatively low metabolic cost compared with mammals and birds (Pianka 1969; Pough 1980; Bradshaw 1986).

Approximately 70% of the Australian continent, which is about five and a half million square kilometres, consists of arid and semi-arid lands. Soon after Europeans first settled in Australia the pastoral industry began to expand into the arid regions of the continent. Because of the harsh and unpredictable climate, cattle and sheep could only survive in areas with permanent or temporary water and stock were moved across the land in search of areas where recent rain had occurred and where plentiful forage was available. Highly productive areas with permanent waters provided refuges for stock when conditions were poor elsewhere and as a result these areas were intensively grazed, whereas many remote areas were rarely utilised. This pattern led Morton (1990) and Stafford Smith and Morton (1990) to hypothesise that over-grazing by sheep and cattle in fertile patches characterised by permanent and reliable water supplies may have reduced heterogeneity in the arid regions of Australia. They proposed that highly productive patches provide vital resources for many native mammals and birds, especially during drought, and that the degradation of these areas may explain the severe range reductions and numerous extinctions that have occurred within the mammal fauna.

More recently, and particularly since the 1950s, large numbers of artificial watering points in the form of dams or bores which access ground water have been installed (Noble & Tongway 1983), enabling more effective use of available forage. This has had the following consequences. First, livestock are able to cover larger areas and access patches of preferred forage which were previously inaccessible because they were remote from water; hence there is further selective grazing of nutrient rich areas. Second, a redistribution of grazing has occurred such that the areas surrounding water
are intensively used, even if these areas contain less preferred forage. Currently about 60% of the arid and semi-arid regions of Australia - approximately three and a half million square kilometres of land - is used for grazing cattle or sheep (see Chapter 2: Figure 2.1). Across this vast area, the density of artificial watering points has become so high that there are very few areas where drinking water is not available to large, mobile vertebrates (Landsberg & Gillieson 1996) and consequently areas that are inaccessible to grazing animals have become rare.

As serious declines in populations of native animals have been documented, the need to conserve biological diversity in the Australian rangelands has become an additional priority alongside the more traditional objective of managing the land so as to maintain future productive potential (Morton et al. 1995). The results of a recent study of the effect of artificial water points on flora and fauna in arid Australia have shown that there are major differences between the composition of plant and animal assemblages at varying distances from water (Landsberg et al. 1997) and that between 15% and 38% of species over several taxonomic groups are less abundant at sites close to water. Although mammals appear to have been most severely affected by changes associated with European settlement (e.g. Morton 1990), it is difficult to assess the extent of impact on other fauna, particularly reptiles, because knowledge of pre-settlement assemblages of these fauna is limited. The few studies that have specifically examined the effect of grazing on reptiles in other parts of the world have indicated that species richness and abundance are lower in heavily grazed areas (Busack & Bury 1974; Jones 1981), possibly due to loss in structural variability.

Mulga shrublands, dominated by *Acacia aneura*, are among the most extensive vegetation communities used by cattle and sheep in arid Australia (see Chapter 2: Figure 2.2), particularly since artificial watering points have become more common. Nevertheless, productivity is relatively low and herbaceous vegetation sparse in mulga shrubland compared with other vegetation communities used for grazing. In central Australia pastoral land is used almost exclusively for grazing cattle. Mulga communities are primarily grazed during dry periods when vegetation is sparse elsewhere (Low et al. 1973) and cattle will generally not travel very far from water in this habitat unless to access distant areas of more preferred forage (Hodder & Low 1978). Because of these factors, some patches of mulga, in areas distant from water, have remained largely undisturbed by grazing animals whereas such remnant areas are difficult to find in other plant communities in the rangelands. Contrasted with heavily grazed mulga close to areas where water has been provided, these distant areas offer a unique opportunity to assess the impact of grazing on the native fauna.
Although mulga shrublands are broadly distributed across the Australian continent, the ecology of the native animals that live in mulga and the manner in which they cope with long dry periods, of indeterminate length, are virtually unknown. Studies of reptiles in this habitat are few (Fyfe 1985; Reid et al. 1993; Preece 1995), and none has specifically examined temporal variations in populations. Forty-five percent of Australian mainland lizard species have part of their range in regions dominated by mulga communities (Beutel 1995) although most of these species have a wide distribution and also occur in other vegetation types (Davies 1973). Beutel (1995) identified clearing, over-grazing and predation by feral carnivores as the major threats to the native reptile fauna in mulga lands.

Degradation in plant communities in rangelands is difficult to quantify because short-term rainfall variability results in dramatic changes in vegetation cover; also, the response of vegetation to rainfall varies in space, as does the impact of grazing (Pickup et al. 1998). Hence, the recent emphasis for determining the extent of degradation has been with the way patterns of vegetation cover change over time and space in response to rainfall and grazing (e.g. Pickup & Chewings 1988; Bastin et al. 1996; Pickup 1996; Pickup et al. 1998). Lizard communities in the Australian arid zone are also characterised by extreme temporal stochasticity (Pianka 1986; James 1994). It is therefore imperative that the effects of climate variability on the activity and abundance of lizards, and on environmental variables which are likely to directly affect lizard activity and abundance, are considered in the assessment of the impact of grazing on these species.

This study was designed to determine the impact of cattle grazing on lizard communities in mulga shrublands with particular emphasis on the relationship between climatic variability and any effect of grazing. Broad objectives of the study were: (a) to identify important factors which structure lizard assemblages in the mulga habitat and particularly those which determine patterns in activity and abundance over time; (b) to contribute to knowledge of the effects of cattle grazing around artificial water points on the Australian native fauna; and (c) to determine the effectiveness of surveys at one point in time in assessing the impact of grazing on lizards in this environment.

This thesis is written as a series of independent papers comprising Chapters 2-6. Because each chapter is written as an independent unit, there is some repetition in the Introduction and Methods sections but I have avoided this to some extent through cross-referencing. A brief outline of the main chapters is given below.

In the first section of the thesis (Chapter 2) I have pooled data collected over 27 months to enable a preliminary comparison of lizard abundance and diversity between
sites with different levels of grazing, and to identify any broad correlations between lizard abundance and structural characteristics of the vegetation or invertebrate biomass at site level.

Because vegetation cover differed among sites, an experimental manipulation of ground vegetation was undertaken to test whether pitfall trapping, the technique used for sampling lizards throughout the study, was equally efficient at sites with different ground cover, and hence whether captures in pitfall traps accurately represented the relative abundance of lizards at different sites. The experiment is described and results are presented in Chapter 3.

Temporal fluctuations in the number of captures of six abundant species over the study period are examined in detail in Chapter 4. Particular emphasis is placed on comparing the timing of activity in different years and interpreting patterns with respect to rainfall, temperature, plant growth and invertebrate abundance. Activity patterns of different species are compared and activity and abundance of lizards at sites with different grazing levels are compared at a number of different time scales to determine whether relative abundance among sites is consistent through time.

In Chapter 5, I examine the relationships between weather conditions during the study, patterns of activity (described in Chapter 4) and rates of growth and body condition of lizards, and determine whether patterns are consistent between sites with different levels of grazing.

In Chapter 6, I look at both temporal and spatial variation in the numbers of lizards captured in relation to changes in vegetation cover. Cover was measured at each site after a dry period and after a period of high rainfall. Differences in cover among sites were not consistent through time so the numbers of lizards captured, at periods corresponding to those when vegetation data were collected, are compared to determine whether changes in relative abundance among sites correspond with the observed changes in vegetation cover. I also present data on the availability of thermal microclimates at different times of the day and in different seasons and examine how these differ between sites depending on the shade produced by the tree canopy.

The sections described above are followed by a synthesis and general discussion (Chapter 7) which includes recommendations for management and future work.
Chapter 2

Lizard assemblages in mulga shrublands in central Australia: Comparison of sites with different levels of grazing
Chapter 2: Lizard assemblages at sites with different levels of grazing

*LIZARD ASSEMBLAGES IN MULGA SHRUBLANDS IN CENTRAL AUSTRALIA: COMPARISON OF SITES WITH DIFFERENT LEVELS OF GRAZING*

**Abstract**

Populations of ground dwelling lizards were monitored for 27 months to determine whether lizard assemblages differ between sites with different grazing levels. The study sites were in mulga (*Acacia aneura*) tall shrubland on a pastoral property in central Australia and sites were categorised as having high or low levels of grazing based on their distance from artificial water points for cattle. Twenty-three species and a total of 2249 individuals were captured during the study. For many species, abundance was highly variable among sites; however, there were several distinct patterns with respect to grazing at both single species and family levels. The agamid *Ctenophorus nuchalis* was found almost exclusively at sites that were close to water points. These sites were characterised by comparatively large areas of open ground, a habitat favoured by this species. In contrast, the total number of skinks captured at sites with low levels of grazing was greater than at sites with high levels of grazing in nine of eleven species and the abundance of skinks as a family group was significantly higher at sites with low levels of grazing. There was a positive correlation between the abundance of skinks and the cover of ground vegetation and the shrub canopy. Differences in vegetation cover among replicate sites within each level of grazing may explain some of the variation between the abundance of skinks at different sites. The abundance of geckos did not differ consistently between sites with different levels of grazing and was not correlated with vegetation cover. Invertebrate biomass did not differ significantly between sites with different grazing levels, and there were no significant relationships between invertebrate biomass and lizard abundance at different sites. There were also no consistent differences in total abundance, species richness or diversity of lizards between sites with different levels of grazing. I conclude that lizards which are active during the day may be more affected by changes in vegetation structure resulting from grazing than nocturnal geckos because they are more directly exposed to extreme temperatures and rely on vegetation for shelter and for providing a range of thermal microhabitats.
Introduction

In Australia, protection of native species that occur primarily on pastoral land is becoming increasingly important as social change leads to a shift in public perception of the importance of conservation (Morton 1993) and the limitations of National Parks and Reserves in fulfilling these roles are recognised (James et al. 1995; Morton et al. 1995). Knowledge of the current distribution and abundance of fauna, especially in relation to patterns of grazing, is a necessary prerequisite if protection of native fauna is to be considered in future management decisions.

Whereas there is little dispute that the expansion of pastoralism in the arid and semi-arid regions of Australia has affected the distribution of many native animals, to date few quantitative data are available. Information about the impact of grazing is limited for all faunal groups (see James et al. in press for a review) and existing work suggests that changes in abundance and community structure are complex and difficult to predict. Most studies of the impact of grazing have been conducted in North America, and among these, studies of reptile communities are particularly scarce. The few studies that have considered reptiles (Busack & Bury 1974; Jones 1981; Bock et al. 1990) have concluded that grazing resulted in lower abundance of some or all species considered. Recently, two studies of reptiles in remnant patches of woodland in Australia have considered different grazing levels as a factor which may contribute to community structure. In Victoria, species richness of reptiles was higher in remnant patches of buloke woodland (Allocasuarina leuhammadii) where past grazing pressure was low (Hadden & Westbrooke 1996), but sheep grazing did not influence species richness of lizards in remnants of eucalyptus woodland in Western Australia (Smith et al. 1996). A reduction in structural variability in the environment has been most frequently cited as being the mechanism for changes in reptile populations resulting from grazing (Busack & Bury 1974; Jones 1981).

The widespread provision of artificial sources of water for stock in the Australian arid and semi-arid zones over the past 150 years has enabled cattle and sheep to access vast areas that were previously inhospitable because of the scarcity of surface water. The radial symmetry of grazing intensity that develops around these water points was first documented in Australia by Osborn et al. (1932), and Lange (1969) introduced the term piosphere (from the Greek word ‘pios’ = to drink) to describe the zones of grazing impact which occur around water points. More recently, clear gradients in vegetation cover radiating from water points have been identified from satellite images (Pickup et al. 1993) and these gradients correspond with ground-based assessments of cover (Bastin et al. 1993). Fencelines restrict the movement of stock and distort radial
patterns of grazing intensity, but generally, grazing is less intense at greater distances from water points within the confines of a paddock. Nevertheless, as the number of water points in the rangelands continues to increase, there are progressively fewer areas that are relatively remote and inaccessible to grazing animals.

The distribution of pastoral land in the arid and semi-arid zones of the Australian continent is shown in Figure 2.1. Mulga (*Acacia aneura*) shrublands are currently one of the most extensive rangeland biomes in Australia (Figure 2.2). Large areas of mulga shrubland in Western Australia and South Australia are used primarily for sheep grazing, but the central Australian pastoral region, in which my study sites are located, is used for cattle grazing (Figure 2.1). I chose areas of tall mulga shrubland with an understorey of predominantly perennial grasses (mulga-perennial: Lendon & Ross 1978) as the focus of my study. Relatively little is known about lizard populations in the mulga shrublands of central Australia compared with other habitats in the semi-arid and arid regions of the continent, particularly in relation to grazing, although there have been a number of basic inventory studies of lizard abundance and diversity (Low & Low 1978; Fyfe 1985; Reid *et al.* 1993; Preece 1995). The radial symmetry of grazing patterns provided the opportunity to use sites that were far from a water point, and infrequently used by cattle, as reference points or controls against which I could assess the effect of grazing in areas close to a water point.

The distance which cattle travel from water is dependent on many factors including season, rainfall, vegetation community and the breed of cattle. In central Australia cattle can travel more than 10 km when feed is sparse and of poor quality (Hodder & Low 1978), but often cattle only graze in mulga shrublands when more preferred forage is scarce (Pickup & Chewings 1988; Chewings *et al.* 1998). A study of cattle distributions on Hamilton Downs Station (where the current study took place), over five years, showed that cattle rarely travel more than 6 km from water, even in dry periods (Pickup & Chewings 1988). Hence, for the purpose of this study I have assumed that grazing levels are low at distances greater than 6 km from a water point.

The climate in central Australia is characterised by hot summers, with temperatures frequently exceeding 40°C, and cool winters, when overnight temperatures can drop below 0°C, and by highly variable and unpredictable rainfall both within and between years. The temporal variation in rainfall is high, on a world scale, for areas of comparable aridity (Stafford Smith & Morton 1990). Average annual rainfall is approximately 270 mm but can range from 60 mm to 782 mm, with yearly totals being skewed towards lower values; the median value for annual rainfall is 236 mm (all data from Bureau of Meteorology, using records from 114 years). The extreme variation in precipitation in the region is reflected in highly variable rates of plant productivity and
Figure 2.1 Distribution of pastoral land in arid and semi-arid Australia and the location of the study area. Adapted from Plumb (1982).
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Figure 2.2 Distribution of mulga shrublands in arid and semi-arid regions of Australia. Adapted from Moore & Perry (1970).
considerable variation in the activity and abundance of animals through time. Reptiles can reduce their metabolic rates and requirements for energy and water consumption dramatically by remaining inactive for long periods when conditions are not favourable, and can also respond rapidly, by resuming activity, when conditions become more favourable. The resulting extreme temporal variability in populations can present problems for sampling and comparing populations in different places because (a) it is difficult to predict when capture rates will be high enough to provide useful data, and (b) simultaneous sampling at different sites is particularly crucial because temporal fluctuations are often more extreme than variation between sites. In addition, and particularly relating to the current study, grazing patterns and the response of vegetation to grazing are known to be variable over time, depending on season and rainfall, and it follows that any differences in lizard assemblages at sites with high and low levels of grazing may also vary through time. I attempted to alleviate some of these problems by sampling at monthly intervals over a 27 month period to obtain a representative sample of ground dwelling lizards at the study sites over a range of seasons and climatic conditions. Rainfall was above the average in 1993 (481.5 mm) and in 1995 (339.8 mm) but was considerably below average (114.8 mm) in 1994. I will consider the temporal variation in the number of lizards captured over this period in detail in Chapters 4, 5 and 6. For the analyses presented in this chapter I have pooled data collected over the entire period to determine whether there were broad and persistent differences between lizard populations at different levels of grazing.

My main objective is to provide information about terrestrial lizard assemblages in mulga woodlands in central Australia at sites with different levels of grazing. Specifically I will address the following questions:

(a) Do the diversity and abundance of lizard assemblages close to artificial water points differ from those of assemblages far from water?
(b) Do the abundances of individual species and groups of species differ between sites close to water and sites far from water?
(c) Does the abundance of lizards correlate with the broad structural characteristics of the vegetation and invertebrate biomass at different sites, and if so, how do these variables differ with distance from water?

Methods

Location of study sites

Hamilton Downs Station, the pastoral property on which the study was undertaken, is located in the centre of Australia in country which is primarily used for cattle grazing (Figure 2.1). Hamilton Downs Station covers 1595 square kilometres, and is
approximately 60 km NW of Alice Springs. The property was chosen for the study because it contains extensive areas of mulga shrubland including areas that are sufficiently far away from water for grazing pressure to be low.

In order to select sites, those areas that were more than 6 km from water were identified from GIS data showing the distribution of water points. Preliminary qualitative examination of possible study areas enabled selection of sites on the criteria that they had similar flora (including height and growth form of acacia shrubs, and composition of shrub and herbage assemblages), soil type, fire history and proximity to geomorphological features. Four lightly grazed sites (more than 6 km from water) and four heavily grazed sites (within 1 km of permanent water) were chosen (Figure 2.3). Each pair of sites (e.g. H1 & L1) was separated by approximately 5 km, and represented two distances along a gradient radiating from a particular water point; however, the spatial distribution of sites and the design of the study was such that each site represented one of four replicate sites with either high or low levels of grazing.

A certain degree of spatial heterogeneity in the landscape was expected; but major differences in lizard assemblages between sites, independent of grazing, were not anticipated prior to the study. Priorities for sampling were (a) to ensure adequate sampling of each site by maximising the number of traps and the area sampled, (b) to replicate samples through time and (c) to maximise the number of replicate areas at each level of grazing. Trade-offs to the design were that there was no replication of sites at each level of grazing, associated with a particular water point. Particular care was taken to ensure that sites on a gradient from a particular water point were similar, based on the qualitative criteria outlined above so that slight variations from place to place were minimised within gradients. Every attempt was made to find eight sites which were as similar as possible with respect to the floristic and structural composition of the vegetation.

There was no information available on the lizard fauna of the area prior to the study and no preliminary trapping was undertaken before establishment of the permanent sites. Hence, sites were chosen at random with respect to knowledge of lizard communities and the habitat requirements of species occurring in the area.

**Trap design and layout**

I installed 40 pit traps, arranged in pairs, at each of the eight trapping sites. Traps in each pair were approximately 9 m apart with 10 m of drift fence erected between the pair, continuing over the pails at each end and extending up to 50 cm beyond. Paired trap units were arranged in a grid of five by four, were approximately 30 m apart and
Figure 2.3 Location of the eight study sites on Hamilton Downs Station showing paddock boundaries and water points. Sites within 1 km of permanent bores (H1, H2, H3, H4) are categorised as having high levels of grazing and sites that are more than 6 km from the nearest water point (L1, L2, L3, L4) are categorised as having low levels of grazing.
were included within an area of approximately 90 m by 120 m. There are no published
data on the home ranges of lizards in mulga shrublands, however, James (1991a)
found that *Ctenotus leonhardii* (one of the most common skinks found in mulga)
moved between 6 and 20 m, on average, depending on the season. I chose a 30 m
spacing between trap units to cover as many lizard home ranges as possible given the
limit on the number of trapping units.

The pit traps were plastic pails, 302 mm in diameter at the mouth and 400 mm deep,
with a sealing lid which I used to close the pit traps between sampling periods. The
pails were buried so that their mouths were slightly below the ground surface.
Fencing material was black, 60% shade cloth. Fences were 300 mm high and were
buried to a depth of approximately 50 mm to ensure lizards could not pass underneath.
The fences were supported by pegs made from lengths of 2 mm diameter wire, spaced
at two metre intervals. The fences were left in place throughout the 27 months of field
work.

**Frequency of trapping and procedures for handling lizards**

I was not able to trap lizards at all eight sites simultaneously because of the distance
between sites and the time required to check traps at each site. During the summer
months it was necessary to have checked all open traps by 1100 h to prevent captured
animals from dying of heat stress. In order to overcome these problems I opened half
of the traps at a time. Traps at the same four sites (H1, L1, H2, L2 and H3, L3, H4,
L4) were always opened together.

All pit traps and fences were installed in August and September 1993. I trapped lizards
at each site, monthly, from October 1993 until December 1995, except for two months
when sites were inaccessible because of high rainfall and local flooding. During each
sampling period traps were opened in the morning of the first day, were checked for
three days, and then closed. I sampled the two groups of sites within a few days of
each other whenever possible and randomised the order in which they were sampled in
each month. Total trapping effort at each site over the 27 months of the study was
3000 pit-trap days.

Trapped lizards were identified, measured and weighed, and each individual (with the
exception of pygopods) was given a unique toe-clip to enable identification in the
future. Lizards were released within a few metres of the trap.
Measurement of environmental variables

I collected macro-invertebrates from the pitfall traps from November 1993 throughout the remainder of the study. Invertebrates were taken back to the laboratory where I identified them to ordinal level, and counted and weighed (± 0.01 g) each individual. I weighed individuals after removing them from 70% alcohol solution and allowing any surface moisture to evaporate. I then calculated the total wet-mass of individuals from each order, captured over the entire study, for each site to derive a relative estimate of biomass for each order. These samples were not intended to represent the availability of prey but were used to derive an index of invertebrate activity and abundance for each of the study sites.

An estimate of canopy cover at each site was derived from measurement of the proportion of the ground that was shaded, not including shade from ground vegetation, when the sun was directly over-head (at approximately 1230 h during December). I placed 10 m of measuring tape along the side of each drift fence used for capturing lizards, and recorded the percent of each transect that was in shade. From these data I calculated the mean cover of canopy across the twenty transects at each site. Shading at each site at different times of the day and year are fully described in Chapter 6.

I also measured cover on the ground at each site in two-hundred 1 m² quadrats, ten in the vicinity of each pair of traps (see Chapter 6 for a more detailed description of methodology). In each quadrat I estimated the cover of standing vegetation (grass, herbs, forbs), small shrubs (< 50 cm high), litter (leaf and grass) and wood (dead branches and logs) and the percent of the ground that was bare. I measured vegetation twice during the study: in September 1994 after a long dry period, and again in June 1995 after a period during which precipitation was higher than average (see Chapter 6). In this chapter I use the mean cover of standing vegetation, litter, wood and bare ground, calculated over the two periods, for comparisons with the abundance of lizards at each site (lizard data are pooled over 27 months). Changes in vegetation cover over time and their relation to lizard abundance are considered in Chapter 6.

Statistical procedures

Rank abundance plots were drawn to give a first indication of the distribution of species abundance at each site. I then calculated Margalef and Berger-Parker indices to give an easily interpretable measure of the abundance and dominance components of diversity at each site (Magurran 1988). I tested for differences in total abundance,
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species richness and the calculated diversity indices between sites with high and low levels of grazing with a series of unpaired t-tests.

At each site, species were assigned to abundance classes based on log₂ (each class is a doubling of species abundances). The expected number of species in each abundance class in a log series distribution was calculated for each site. I used a Chi-squared goodness of fit test to compare expected and observed abundances to determine how well lizard assemblages at each site fitted a log series model. Procedures outlined in Magurran (1988) were followed.

I tested whether the abundance of individual species and of family groups differed between sites with high and low levels of grazing with unpaired t-tests. I used correlation analyses to test for simple relationships between lizard abundance, at the level of family, with the following variables: invertebrate biomass, tree and shrub canopy, the cover of ground vegetation, litter and wood and the percent of bare ground at each site.

Data for lizard captures, invertebrate biomass, and ground cover were not normally distributed and the following transformations were applied prior to all analyses. Lizard captures and invertebrate biomass were transformed by log₂(x + 1). An arcsin transformation was applied to estimates of percentage canopy cover and bare ground. A square root transformation (sqrt (x + 1/2)) was used for data on percentage wood, ground vegetation, litter and shrub cover, because values were low for these variables (< 20%) and the square root transformation is appropriate under these circumstances (Steel & Torrie 1980).

Multi-dimensional scaling was applied to the data for each species at each site (a matrix of 23 species by 8 sites), using the Semi Strong Hybrid module of PATN (Belbin 1991a, b), and the Bray-Curtis similarity measure. This statistic calculated a similarity index between each pair of sites based on the abundance and presence or absence of different species and then plotted all sites in three dimensional space based on their respective Euclidean distances. That is, sites at which the relative abundance of the 23 species of lizards were more similar plotted closer together. The stress value is a measure of how difficult it is to present the data in this way and how well the relationship between sites can be expressed in three dimensions according to the variables included. The distribution of sites in three dimensional space can be tentatively examined to determine whether sites fall out in a pattern which corresponds to known variation among sites, independent of the variables used in the analysis.
Results

Lizard abundance and diversity in relation to grazing

Twenty three lizard species and a total of 2249 individuals were captured during the study, not including recaptures of previously marked individuals which accounted for an additional 176 captures. Three abundant species accounted for 95% of recaptures and there was no significant difference in the number of recaptures between heavily and lightly grazed sites \( t_{\text{stat}} = 1.96, P = 0.10 \). It was not possible to fit population models or to estimate abundance at each site because the number of recaptures was low. The number of captures of each species, not including recaptures, provided an index of relative abundance of lizards at each site, which I used for all analyses. The numbers of individuals of each species captured at each site are listed in Table 2.1.

Most of the captures were of small, ground dwelling lizards, with occasional captures of arboreal species such as the gecko Gehyra variegata. These arboreal species almost certainly occurred in much greater abundance than is indicated by capture rates. Several other species, including the large and mobile goanna Varanus gouldii which was sighted several times during the study, were not captured at all. Hence, there is a distinct bias in pitfall traps toward capturing particular species. Ctenotus schomburgkii and Ctenotus leonhardii were the most frequently captured species. Variation in abundance among sites was high for almost all species and this was particularly apparent for the species captured most frequently.

No obvious differences are apparent between rank abundance plots for sites with different levels of grazing (Figure 2.4) although sites H1 and H3 were dominated by three relatively abundant species (10-100 captures) whereas there were between four and six abundant species at the other sites. Plots for sites H1 and H3, as well as sites L1 and L3, fall below those of the other sites and this reflects generally lower abundance at these sites, particularly for those species with intermediate abundance, and hence possibly a less even distribution of species abundances compared with the other sites.

Rank abundance plots appeared generally to fit a log-series distribution. Goodness of fit tests showed that the species abundance distribution for two of the sites could be described by the log series model with 70% confidence (L1: \( \chi^2_{\text{stat}} = 3.47, P > 0.70 \), H3: \( \chi^2_{\text{stat}} = 3.69, P > 0.70 \)). There was no significant difference between the observed distribution of abundances and those expected in a log series distribution at the other sites either, but probabilities were lower than for sites L1 and L3. This suggests that the log series can be used to describe the distribution of species abundances at all the
Table 2.1 Species and numbers of lizards captured at each site between October 1993 and December 1995. Data do not include recaptures.

<table>
<thead>
<tr>
<th>Species</th>
<th>High grazing</th>
<th>Low grazing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H1</td>
<td>H2</td>
</tr>
<tr>
<td>GEKKONIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplodactylus ciliaris</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Diplodactylus conspicillatus</td>
<td>18</td>
<td>22</td>
</tr>
<tr>
<td>Diplodactylus stenodactylus</td>
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<td>13</td>
</tr>
<tr>
<td>Gehyra variegata</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Heteronotia binoei</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Nephrurus levis</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rhyndroedura ornata</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>PYGOPODIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delma tincta</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pygopus nigriceps</td>
<td>6</td>
<td>-</td>
</tr>
<tr>
<td>AGAMIDAE</td>
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<td></td>
</tr>
<tr>
<td>Ctenophorus nuchalis</td>
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</tr>
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<td>Lophognathus ilberti</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Pogona vitticeps</td>
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<td>2</td>
</tr>
<tr>
<td>SCINCIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carlia munda</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cryptoblephanus plagiocephalus</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ctenotus leonhardii</td>
<td>84</td>
<td>15</td>
</tr>
<tr>
<td>Ctenotus schomburgkii</td>
<td>82</td>
<td>92</td>
</tr>
<tr>
<td>Egermia insurnata</td>
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<td>-</td>
</tr>
<tr>
<td>Eremiascincus richardsonii</td>
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<td>1</td>
</tr>
<tr>
<td>Lerista desertorum</td>
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<tr>
<td>Lerista labialis</td>
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<tr>
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<tr>
<td>Menetia greyii</td>
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<td>Morethia ruficauda</td>
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Figure 2.4 Rank abundance plots for lizard species at sites with high and low levels of grazing.
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sites but the model is a closer fit to the observed distribution at sites L1 and H3 compared to the other sites.

Species richness (the total number of species captured) and Margalef and Berger-Parker indices of diversity for the eight sites are listed in Table 2.2. Species richness at sites varied between 14 and 17, and there was no consistent difference between sites with different grazing levels ($t_{adj} = -0.31, P = 0.77$). No differences between either of the diversity measures were detected between sites with high and low levels of grazing (Margalef index: $t_{adj} = 0.57, P = 0.59$, Berger-Parker index: $t_{adj} = 0.16, P = 0.70$).

Before testing for differences in captures of each species between sites with different grazing levels I pooled data for species that were captured very infrequently ($< 20$ captures) to maximise the sample size used for analysis and the confidence in the statistic. Only two significant differences between lizard abundance at sites with different levels of grazing were detected (Table 2.3). The agamid *Ctenophorus nuchalis* was only captured once in a lightly grazed site but was captured at each of the sites close to water, being particularly abundant at site H2 (Table 2.1). The infrequently captured species, when pooled, were consistently more abundant at lightly grazed sites (Table 2.3). Coefficients of variation (Table 2.3) were very high because abundance of most species varied considerably between sites. As a result of this variability, and the limited number of sites sampled, the power to detect deviations from the null hypothesis was limited.

Data for species within each of the three most abundant family groups, geckos, agamids and skinks, were pooled for further analysis. Data for infrequently captured species were omitted from pooling at family level. These data would have contributed very little, numerically, to totals for family groups, yet from an ecological perspective rare species may be important; therefore, I decided to continue to consider these species as a separate group. Sample size for each site was higher and variance between sites was lower when data were pooled at the family level. Hence, the analyses using family groups were more likely to detect differences between sites with different grazing levels, if these existed, than when individual species were considered.

There were distinct differences between family groups with respect to their relative abundance at sites with different grazing levels (Figure 2.5). The number of geckos captured did not differ significantly between sites with different grazing levels ($t_{adj} = 0.88, P = 0.41$). Agamids were more abundant at sites with high levels of grazing ($t_{adj} = 2.42, P = 0.05$) and, in contrast, skinks were consistently more abundant at sites
Table 2.2 Diversity and abundance of lizard assemblages at the eight study sites: Total number of lizards captured (N) not including recaptures; species richness (SR); the Margalef index (Dmg); and the Berger Parker index (d). Means and standard deviations are given for sites with high (prefix H) and low (prefix L) levels of grazing.

<table>
<thead>
<tr>
<th>Site</th>
<th>N</th>
<th>SR</th>
<th>Dmg</th>
<th>1/d</th>
</tr>
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<tbody>
<tr>
<td>H1</td>
<td>222</td>
<td>14</td>
<td>2.41</td>
<td>2.64</td>
</tr>
<tr>
<td>H2</td>
<td>293</td>
<td>15</td>
<td>2.46</td>
<td>3.18</td>
</tr>
<tr>
<td>H3</td>
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<tr>
<td>H4</td>
<td>282</td>
<td>14</td>
<td>2.30</td>
<td>2.82</td>
</tr>
<tr>
<td>Mean (SD)</td>
<td>245 (52)</td>
<td>15 (1)</td>
<td>2.47 (0.16)</td>
<td>2.66 (0.50)</td>
</tr>
<tr>
<td>L1</td>
<td>288</td>
<td>14</td>
<td>2.30</td>
<td>2.34</td>
</tr>
<tr>
<td>L2</td>
<td>442</td>
<td>17</td>
<td>2.63</td>
<td>2.34</td>
</tr>
<tr>
<td>L3</td>
<td>218</td>
<td>14</td>
<td>2.41</td>
<td>1.91</td>
</tr>
<tr>
<td>L4</td>
<td>324</td>
<td>14</td>
<td>2.25</td>
<td>3.38</td>
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<tr>
<td>Mean (SD)</td>
<td>318 (94)</td>
<td>15 (2)</td>
<td>2.40 (0.17)</td>
<td>2.49 (0.63)</td>
</tr>
</tbody>
</table>

H: high grazing
L: low grazing
Table 2.3 Comparisons of lizard abundances between sites with high and low levels of grazing. Data are results of unpaired t-tests (df = 6). The coefficient of variation (CV) is given for sites with high (H) and low (L) levels of grazing for each species. Significant differences \( (P \leq 0.05) \) are marked (*)

Data were log transformed before analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean difference (high - low)</th>
<th>( t ) value</th>
<th>( P ) value</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GEKKONIDAE</strong></td>
<td></td>
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<td></td>
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<tr>
<td>Diplodactylus ciliaris</td>
<td>-0.21</td>
<td>-0.94</td>
<td>0.38</td>
<td>26</td>
</tr>
<tr>
<td>Diplodactylus conspicillatus</td>
<td>-0.04</td>
<td>-0.07</td>
<td>0.95</td>
<td>116</td>
</tr>
<tr>
<td>Diplodactylus stenodactylus</td>
<td>0.23</td>
<td>0.82</td>
<td>0.45</td>
<td>41</td>
</tr>
<tr>
<td>Gehyra variegata</td>
<td>0.11</td>
<td>0.82</td>
<td>0.44</td>
<td>31</td>
</tr>
<tr>
<td>Rhynchoedura ornata</td>
<td>-0.23</td>
<td>-0.74</td>
<td>0.49</td>
<td>47</td>
</tr>
<tr>
<td><strong>PYGOPODIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pygopus nigriceps</td>
<td>-0.29</td>
<td>-1.35</td>
<td>0.22</td>
<td>83</td>
</tr>
<tr>
<td><strong>AGAMIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenophorus nuchalis</td>
<td>1.27</td>
<td>4.58</td>
<td>0.004*</td>
<td>40</td>
</tr>
<tr>
<td>Lophognathus gilberti</td>
<td>-0.07</td>
<td>-0.46</td>
<td>0.66</td>
<td>18</td>
</tr>
<tr>
<td>Pogona vitticeps</td>
<td>0.11</td>
<td>0.61</td>
<td>0.56</td>
<td>30</td>
</tr>
<tr>
<td><strong>SCINCIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenotus leonhardii</td>
<td>-0.29</td>
<td>-1.48</td>
<td>0.19</td>
<td>22</td>
</tr>
<tr>
<td>Ctenotus schomburgkii</td>
<td>-0.11</td>
<td>-0.65</td>
<td>0.54</td>
<td>9</td>
</tr>
<tr>
<td>Lerista labialis</td>
<td>-0.29</td>
<td>-0.61</td>
<td>0.57</td>
<td>78</td>
</tr>
<tr>
<td>Menetia greyii</td>
<td>-0.08</td>
<td>-0.31</td>
<td>0.77</td>
<td>57</td>
</tr>
<tr>
<td>Morethia ruficauda</td>
<td>0.28</td>
<td>0.58</td>
<td>0.58</td>
<td>65</td>
</tr>
<tr>
<td><strong>Rare species</strong></td>
<td>-0.48</td>
<td>-3.03</td>
<td>0.02*</td>
<td>55</td>
</tr>
</tbody>
</table>
Figure 2.5  Mean captures (±SE) of geckos, skinks, agamids and rare species at sites with high and low grazing levels. Rare species were those which were infrequently captured (< 20 captures at all sites over the entire period of study) and were not included when data were pooled according to family.
Chapter 2: Lizard assemblages at sites with different levels of grazing

with low levels of grazing ($t_{df} = -1.84, P = 0.05$). Results for the infrequently captured species are also shown (Figure 2.5).

The relative abundance of geckos at different sites was not consistent among species (Table 2.1). The abundance of some species was notably uneven across sites, but this variation did not correspond to grazing level. For example *Diplodactylus conspicillatus* was frequently captured at sites H1, H2, L1, L2 but not at the other four sites, whereas *Rhynchoedura ornata* was most frequently captured at sites L3, L4 and H4. Several other species were relatively uniformly abundant among sites whereas *Heteronotia binoei* was captured more frequently on lightly grazed sites ($t_{df} =-3.73, P < 0.01$), although captures were very low for this species and this result should be interpreted with caution.

Agamid species also did not show consistent trends in their distribution relative to different grazing levels despite the fact that, when all species were considered together, the number of agamids captured was significantly greater at sites close to water. *Ctenophorus nuchalis* was by far the most frequently captured agamid and the result at family level is largely influenced by this species. There was no evidence that the other agamid species differed in abundance at sites with different levels of grazing (Table 2.1).

In contrast to the other family groups, skinks showed a consistent trend across most species with respect to their abundance at sites with different grazing levels. Mean captures at sites with low grazing were higher for all except two species (Table 2.1) which were only captured at one or two sites each and in very low numbers.

**Correlations with environmental variables**

Mean biomass of each invertebrate order at sites with high and low levels of grazing is shown in Table 2.4. There were no significant differences between biomasses of any order at sites with different grazing levels or when all invertebrate orders were pooled ($t_{df} = -0.45, P = 0.67$).

Estimates of the cover of ground vegetation at each site are plotted against canopy cover in Figure 2.6 (a) and provide a simple characterisation of each site with respect to these variables. Cover of ground vegetation was generally lower at sites with high levels of grazing, although there was some overlap with site L3. Canopy cover was higher at all of the sites with low grazing levels although the variation between sites, within the two levels of grazing, was considerable. The difference in general structural characteristics at sites with high and low levels of grazing is very clear when estimates of the percent of open ground at each site are plotted against canopy cover (Figure 2.6).
Table 2.4 Invertebrate orders collected from pitfall traps over 27 months showing mean biomass and standard deviations (SD) at sites with high and low levels of grazing. \( N = 4 \) sites each for high and low grazing.

<table>
<thead>
<tr>
<th>Order</th>
<th>Mean biomass (g)</th>
<th>SD</th>
<th>Mean biomass (g)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High grazing</td>
<td></td>
<td>Low grazing</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Araneae</td>
<td>19.64</td>
<td>7.04</td>
<td>25.05</td>
<td>9.60</td>
</tr>
<tr>
<td>Blattodea</td>
<td>14.04</td>
<td>4.51</td>
<td>12.13</td>
<td>7.80</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>82.57</td>
<td>49.33</td>
<td>85.64</td>
<td>69.78</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>0.55</td>
<td>0.64</td>
<td>0.31</td>
<td>0.08</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>0.99</td>
<td>0.50</td>
<td>1.33</td>
<td>1.24</td>
</tr>
<tr>
<td>Isopoda</td>
<td>0.02</td>
<td>0.04</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>0.33</td>
<td>0.45</td>
<td>0.12</td>
<td>0.21</td>
</tr>
<tr>
<td>Mantodea</td>
<td>1.38</td>
<td>2.46</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>16.28</td>
<td>4.19</td>
<td>10.93</td>
<td>5.75</td>
</tr>
<tr>
<td>Phasmatoidea</td>
<td>0.87</td>
<td>0.56</td>
<td>0.66</td>
<td>0.47</td>
</tr>
<tr>
<td>Scoleopendrida</td>
<td>44.36</td>
<td>9.80</td>
<td>40.48</td>
<td>35.36</td>
</tr>
<tr>
<td>Scorpionida</td>
<td>71.29</td>
<td>21.52</td>
<td>89.04</td>
<td>38.67</td>
</tr>
<tr>
<td>Scutigerida</td>
<td>0.34</td>
<td>0.61</td>
<td>0.12</td>
<td>0.21</td>
</tr>
<tr>
<td>Thysanura</td>
<td>0.02</td>
<td>0.03</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>unidentified larvae</strong></td>
<td><strong>3.59</strong></td>
<td><strong>2.43</strong></td>
<td><strong>14.75</strong></td>
<td><strong>19.77</strong></td>
</tr>
</tbody>
</table>

24
Figure 2.6 (a) The relationship between the cover of ground vegetation and canopy cover at the study sites. (b) The relationship between the percentage of bare ground and canopy cover at the study sites. Sites with high levels of grazing are indicated by open circles and sites with low levels of grazing by closed circles.
b). The sites close to a water point are all characterised by relatively large areas of open ground and less canopy cover compared to the other sites.

The abundance of geckos, skinks and agamids at each site was compared with the measured environmental variables. Significance levels for correlations were adjusted according to the Bonferroni inequality \((0.05/n, \text{ where } n = \text{ the number of variables tested})\) to compensate for the increased chance of type 1 error associated with multiple comparisons. *Ctenophorus nuchalis* and *D. conspicillatus* were omitted from these analyses and considered separately because their complete absence at a number of sites and high abundance at others were likely to strongly affect totals for families. The numbers of geckos and agamids captured were not significantly correlated with any of the measured variables, but the abundance of skinks was positively correlated with the cover of ground vegetation and with canopy cover (Table 2.5).

Canopy cover and cover of ground vegetation were correlated at the study sites \((r = 0.78, P = 0.02; \text{ Figure 2.6 a})\), so it is not immediately obvious which, if either, of these variables is directly related to the abundance of skinks. The numbers of skinks captured in each paired trap-unit were compared with estimates of ground vegetation cover and canopy cover measured at each trap to determine whether correlations were detectable at this scale. There was a positive correlation between lizard captures and the cover of ground vegetation at each trap \((r = 0.44, P < 0.0001)\) whereas there was no relationship between canopy cover and lizard captures at the trap level \((r = 0.04, P = 0.58)\). These results suggest that it is more likely that there is a functional relationship between skink abundance with vegetation at ground level than with the canopy.

The variation in ground vegetation at sites within and between the different levels of grazing corresponded to the variation in skink captures (Figure 2.7 a). Of the lightly grazed sites, the site that had the least cover of ground vegetation (L3) had the lowest skink captures. Correspondingly, among sites with high levels of grazing, sites H1 and H4 had the highest cover of ground vegetation and skinks were captured most frequently at these sites.

The abundance of the gecko *D. conspicillatus* was not correlated with any of the measured environmental variables. *Ctenophorus nuchalis* was positively correlated with the percentage of bare ground \((r = 0.83, P = 0.01; \text{ Figure 2.7 b})\) and negatively correlated with the cover of ground vegetation \((r = -0.83, P = 0.01)\). These two variables are inversely correlated and both differ between sites with high and low grazing. Nevertheless, it is clear from Figure 2.7 (b) that the percentage of bare
Table 2.5 Correlations between the abundance of lizard families and environmental characteristics.
Data are correlation coefficients (r) and N = 8 for all correlations. Significant results at (P < 0.007) as calculated using the Bonferroni inequality are indicated with an asterisk.

<table>
<thead>
<tr>
<th></th>
<th>Skinks</th>
<th>Geckos</th>
<th>Agamids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Invertebrate biomass</td>
<td>-0.25</td>
<td>-0.01</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>P = 0.56</td>
<td>P = 0.97</td>
<td>P = 0.50</td>
</tr>
<tr>
<td>Canopy (% cover)</td>
<td>0.86*</td>
<td>0.16</td>
<td>-0.09</td>
</tr>
<tr>
<td></td>
<td>P = 0.004</td>
<td>P = 0.72</td>
<td>P = 0.83</td>
</tr>
<tr>
<td>Bare ground</td>
<td>-0.68</td>
<td>-0.12</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>P = 0.07</td>
<td>P = 0.78</td>
<td>P = 0.70</td>
</tr>
<tr>
<td>Litter (% cover)</td>
<td>0.12</td>
<td>0.16</td>
<td>-0.50</td>
</tr>
<tr>
<td></td>
<td>P = 0.79</td>
<td>P = 0.72</td>
<td>P = 0.22</td>
</tr>
<tr>
<td>Ground vegetation (% cover)</td>
<td>0.86*</td>
<td>0.09</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>P = 0.003</td>
<td>P = 0.85</td>
<td>P = 0.50</td>
</tr>
<tr>
<td>Wood (% cover)</td>
<td>-0.09</td>
<td>-0.33</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>P = 0.84</td>
<td>P = 0.44</td>
<td>P = 0.02</td>
</tr>
<tr>
<td>Shrub (% cover)</td>
<td>-0.53</td>
<td>-0.29</td>
<td>-0.26</td>
</tr>
<tr>
<td></td>
<td>P = 0.19</td>
<td>P = 0.51</td>
<td>P = 0.56</td>
</tr>
</tbody>
</table>
Figure 2.7  (a) The relationship between the number of skinks captured and the cover of ground vegetation at the study sites.  (b) The relationship between the number of *Ctenophorus nuchalis* captured and the percentage of bare ground at the study sites.
ground cannot fully explain the relative abundance of *C. nuchalis* among sites with high levels of grazing.

**Structure of lizard assemblages**

Multi-dimensional scaling of the site-by-species data matrix revealed a three-dimensional structure in the data (stress value = 0.09). Data are presented in three planes in two dimensions in Figure 2.8.

The distribution of sites along the axis representing dimension 2 (Figure 2.8 a & c) corresponds with different levels of grazing; the four sites close to water and those far from water fall out in two non-overlapping planes. This pattern indicates that a degree of similarity between sites with the same level of grazing can be detected, when all species are considered, which essentially supports the hypothesis around which this study was based. Because I was primarily interested in long-term effects of grazing I did not quantify the short-term intensity of grazing at individual sites. However, I did observe that L3 was used by cattle on several occasions during the study, unlike the other sites categorised as having low levels of grazing. This site also had the lowest percentage cover of ground vegetation among the sites with low levels of grazing, whereas site H1 had the highest cover of ground vegetation among the sites with high grazing levels (see Figure 2.6 a). The similarity between lizard assemblages at sites L3 and H1, as represented by their proximity along dimension 2, may in part be accounted for by the similarity in vegetation cover at these sites. The other sites show clearer separation between different levels of grazing.

Other patterns were also apparent; sites H1, L1, H2, L2 and H3, L3, H4, L4 separate along the first axis of multi-dimensional space (Figure 2.8). These two groups of sites are those that were sampled at different times in each month, but also sites H1, L1, H2, L2 are located further to the west than the other four sites (Figure 2.3). The temperatures on days when sites in each group were sampled were compared and no consistent differences were evident (unpublished results), but even slight differences in weather conditions, resulting from surveys being off-set by several days, may have influenced the rate of capture of some species. With the data available it is impossible to separate any such effects of time from other factors, such as location, which may account for the separation of these groups.

In dimension 3 sites H1, L1, H3, L3 fall out close together. A degree of similarity between lizard assemblages at these sites was also apparent from rank abundance plots (Figure 2.4) but an explanation for this is not obvious from available data. Pairs of sites associated with a particular watering point (e.g. H1 & L1, H4 & L4) plot closely
Figure 2.8 Three planes of a single three-dimensional plot resulting from multi-dimensional scaling of data for abundance of 23 lizard species at the study sites. Open circles indicate sites with high levels of grazing, closed circles are sites with low levels of grazing. Site labels are given, omitting site prefixes H and L.
together in the first and third dimension. This may be because these sites are relatively close in geographical space, and when sites were chosen some attempt was made to ensure that vegetation structure was broadly similar within these pairs (see Methods, this chapter).

**Discussion**

Data presented in this chapter were collected over a period of 27 months, which included four seasons and periods with high and low rainfall. The numbers of lizards captured over this period were highly variable through time; lizards were generally more active when temperatures were high and when conditions were comparatively mesic. Some species were abundant early in the study but rarely captured in the final year whereas others increased in abundance over the period. Because of the range of seasons and weather conditions during the study I am confident that most of the species present at the study sites that are likely to be captured in pitfall traps were represented in the data. Twenty-three species were recorded, which is a greater number than has been previously reported from mulga sites in central Australia (Fyfe 1985; Preece 1995). The true number of species occurring at the sites was even greater (e.g. *Varanus gouldii* was sighted), but not all species were captured because the trapping technique was biased toward small ground-active lizards. By pooling data over the entire period, I was able to make simple comparisons of lizard assemblages between sites with different levels of grazing and to consider the less commonly captured species as well as abundant species in assessment of the differences or similarities between sites. I discuss temporal variability in captures of the most abundant species and the impact of grazing in the context of this variability in subsequent chapters.

In an environment that is characterised by long dry periods, and where surface water is rarely available, the provision of permanent water sources is significant, not only because grazing is intensified in the areas surrounding water, but also, because the water can be used directly by some animals. For example, kangaroos drink from cattle troughs during dry periods (Newsome 1965a; Caughley & Grigg 1982) as well as benefiting directly from changes in the vegetation resulting from grazing (Newsome 1965a, b). There is evidence that water-dependent birds such as the emu, galah, zebra finch, and the crested pigeon have increased in abundance or range in the arid zone in response to the provision of water (Reid & Fleming 1992) and artificial waters may also provide a focus for hunting and drinking by predators like the dingo, fox and feral cat (see James *et al.* *in press*).
A large proportion of birds, small mammals and reptiles which are native to the arid lands of Australia do not require drinking water and so do not benefit directly from the widespread provision of water. These species are able to obtain sufficient water for survival from their diet and have the capacity to persist despite dramatic fluctuations in populations in response to variable conditions. If the expansion of pastoralism and provision of water affect these species the causes are likely to be indirect; for example, through changes in the abundance of competitors, predators or prey species or through changes to the structure of vegetation and other characteristics of the physical environment.

Lizards are one group of animals which are unlikely to be directly affected by grazing animals or the provision of water itself, although trampling may cause damage to burrows and lizards sheltering in burrows. The ability of reptiles to remain inactive for long periods and so dramatically reduce energy expenditure when environmental conditions are sub-optimal enables them to be universally successful in deserts, in terms of their numbers and species richness (Pianka 1986). These same characteristics could lead to the prediction that lizards are one of the vertebrate groups least likely to be affected by grazing. However, at the sites monitored in this study, there were differences in the abundance of lizards in areas close to and distant from water at both species and family levels. These differences provide evidence that the widespread provision of water and associated levels of grazing may have had an effect on reptiles over a large area.

Before I discuss in detail the differences between lizard assemblages at sites with different grazing levels, a few general points about the strength of the results presented here are pertinent. The high variability in lizard abundance among sites, the low number of replicate sites at the two levels of grazing ($n = 4$), and the low number of captures of many species limited the power of statistical tests to identify departures from the null hypothesis that there were no differences between sites with different grazing levels. For frequently captured species, consideration of patterns of abundance over time add crucial information to the results presented here (Chapters 4, 5 & 6), but I was not able to analyse data for uncommon species in this way.

Because I categorised sites based on their proximity to water points, the precise level of grazing differed, both historically and during the study, among the replicate sites close to and distant from water. Combined with background spatial variation, this may account for some of the variation in lizard abundance among replicate sites and may have made it more difficult to identify any response of lizards to grazing. Despite the variability which selecting sites in this way introduces, assessing whether there are any general impacts around water points may be more useful than comparing grazed areas.
with completely ungrazed areas in reserves and National Parks, particularly in the context of conservation off-reserves. My aim was to identify any broad patterns in the distribution and abundance of native fauna which relate directly to management practices. Once identified, such generalised patterns provide tangible information for land managers and can also lead to specific and workable recommendations for management in the future.

As more information about spatial and temporal variability in the abundance of lizards becomes available (see also Chapters 4, 5 and 6), both in mulga shrublands and other habitats, and expected effects of grazing on lizards can be predicted, studies can be designed to have appropriate power to test specific hypotheses. The results presented here are important because this study identifies trends for differences in abundance of lizards between sites with different grazing levels, and the results provide a basis for identifying clear hypotheses to be tested in the future.

**The abundance of different species of lizard in relation to grazing**

Perhaps the most obvious difference between sites with different grazing levels was that the agamid *Ctenophorus nuchalis* occurred almost exclusively at sites close to a water point. This species typically occurs in very open areas (Heatwole 1970; Pianka 1971a) and high populations have been observed in other disturbed environments such as cleared road verges (Bradshaw 1981) and in areas which have been recently burnt (Baker et al. 1993). Areas which are in a permanently low seral state may be refugia in which populations of *C. nuchalis* persist, and from which they invade new habitats and are able to rapidly establish large populations (Bradshaw 1981). In my study *C. nuchalis* was more abundant at sites with high levels of grazing, which were generally more open, but abundance varied substantially among replicate sites (Figure 2.7 b). The area of bare ground alone cannot explain the patterns of relative abundance at sites with high levels of grazing. Site H2, where the abundance of *C. nuchalis* was highest, did not have more bare ground than the other sites close to water. The skink *Ctenotus leonhardii*, in contrast to *C. nuchalis*, was least abundant at H2 and there was an inverse relationship between the number of captures of the two species across all sites (Table 2.1). It is possible that these species interact competitively.

The two other agamid species *Pogona vitticeps* and *Lophognathus gilberti* appear to have been uniformly distributed with respect to grazing level. Hence the pattern observed for *C. nuchalis* did not represent a consistent trend among the agamids.

The lower abundance of skinks, when considered as a family, at sites with high levels of grazing reflected trends observed for individual species and suggests that all species
in this group responded in a similar way to changes associated with grazing. At first this may seem counter-intuitive; some species are fossorial or litter dwellers (e.g. genus *Lerista*), others such as the two species of *Ctenotus* are surface active. But all the skinks that I captured are similar in that they are predominantly diurnal, active foragers. The abundance of skinks was positively correlated with the cover of ground vegetation, so the effect of grazing on plant cover may explain some of the differences between the numbers of skinks captured at sites with different grazing levels as well as some of the variation within each grazing level. Vegetation cover can directly affect temperatures on the ground during the day and may be particularly important in providing shelter from extremely high temperatures in summer. The abundance and activity of all skinks, regardless of their particular habits, may have been affected by differences in the thermal environment at different sites. Of course this does not explain all the patterns in the abundance of skinks observed in this study, but it is consistent with the observation that geckos showed no general trends in their distribution with respect to different grazing levels or general structural components of the vegetation. Geckos captured during the study are all nocturnal and differences in plant cover would have had less effect on temperatures on the ground during the active period for these species. If verified, the link between the abundance of some species and vegetation cover will be a valuable management tool, because predictions about the effect of grazing on a range of species could be made based on surrogate factors, which are more easily measured than actual populations.

Vegetation cover, both on the ground and at canopy level, was the only measured environmental variable which was significantly correlated with the abundance of any lizard species or family group. Perhaps surprisingly, no relationship between the biomass of invertebrates and the abundance of lizards was found. During exploratory analyses, I tested for correlations between each lizard species and the abundance and biomass of each invertebrate order. I have not presented these results because there were numerous comparisons, and for many lizard species and invertebrate orders captures were few so confidence in the results was limited. Additionally, because I had no data on which invertebrates comprised dominant prey for particular lizard species, links between lizard and invertebrate abundance at this level are purely speculative. A further complicating factor is that invertebrates were collected from the same traps used to capture lizards, so they were susceptible to being eaten by lizards which were captive at the same time. Hence the number of invertebrates collected at sites where many lizards were captured may have been comparatively fewer than the number present at that site. The body condition of lizards is probably a better indicator of the availability of prey than estimates of abundance based on individuals collected from pitfall traps. I will examine changes in body condition over time and make
comparisons of the condition of lizards between sites with different grazing levels in Chapter 5.

Many studies which have been designed specifically to determine the effect of grazing on invertebrate communities have found clear and often dramatic differences in abundance and species composition between grazed and ungrazed areas (e.g. Boyd 1960; Cloudsley-Thompson & Idris 1964; Abensperg-Traun et al. 1996). These studies all report a complex range of responses by different components of the fauna. Beetles are one group which may increase in abundance in grazed areas (Abensperg-Traun et al. 1996) whereas grass-hoppers, which are directly associated with grass cover, are generally less diverse and abundant in grazed areas (Fielding & Brusven 1995), although response differs widely among genera. Yet these trends relating to particular invertebrate orders were not evident at my sites. It is possible that overall abundance and biomass of invertebrates did not differ between sites with different grazing levels, as my results suggest, even if there were changes in species composition and relative abundance which I could not detect. Most of the lizards I captured feed on a wide range of invertebrate prey; hence, differences in the composition of invertebrates may not be important provided the total availability of prey is sufficient. It is likely that dramatic fluctuations in invertebrate abundance over time have a comparatively greater effect on the activity and abundance of lizards than relatively small differences in prey abundance and composition among sites. I consider this further in Chapters 4 and 5.

The species which were captured infrequently were not necessarily uncommon at the sites but, compared with other species, they may have been less susceptible to the method of trapping. Nevertheless, only one of these species was arboreal, and there is no reason to expect that the others were less susceptible to falling into pitfall traps than the other terrestrial and fossorial species which were captured more frequently. Additionally, only one of the species was recorded in mulga 100 km north of the Hamilton Downs (Preece 1995), so it is likely that these species were truly relatively uncommon. Many of the animals that occur in mulga shrublands have wide distributions and can tolerate a wide range of climates (Davies 1973) and there are few lizard species which occur only in mulga and not in other vegetation communities. All of the lizards captured during this study fit this description, including those which were captured infrequently. Nevertheless, the relative abundance of different species in mulga may reflect how effectively a species can exploit this environment. The lower abundance of the uncommon species, collectively, at sites with high levels of grazing may suggest that species which are only marginally successful in this habitat are less
likely to persist in heavily grazed areas. If true, this is an important result, irrespective of the distribution and abundance of these species in other habitats.

**The structure of lizard assemblages in relation to grazing**

Diversity indices and rank abundance plots did not indicate that there were any consistent differences between the structure of lizard assemblages captured in this study with respect to differences in grazing intensity. However, multi-dimensional scaling analysis confirmed that it was possible to distinguish between sites with different grazing levels when the abundance of all species at each site is considered. The separation of sites with different grazing levels in three dimensional space can be attributed in part to some of the differences among individual species and groups which have been discussed above.

Variability in the numbers of lizards captured at the eight sites, in what appeared to be similar areas of mulga shrubland, was high. Sites with high levels of grazing did not universally have a high abundance of skinks or low abundance of *C. nuchalis*; nevertheless, changes in the structural environment resulting from grazing appear to favour or disadvantage certain species. Further work is required to confirm the relationship between the abundance of individual species and the structural characteristics of the vegetation. The consistent trends among functional or taxonomic groups in their response to different levels of grazing and to structural differences in vegetation are encouraging; they enable the formulation of specific hypotheses to explain the mechanisms by which pastoralism affects populations of lizards in this habitat, based on commonalities between species which make up response groups. This is undoubtedly the way forward, so that future management decisions can be made based on sound predictions about their effects on a range of species.
Chapter 3

The effect of vegetation cover on rates of capture of ground-active lizards in pitfall traps
THE EFFECT OF VEGETATION COVER ON RATES OF CAPTURE OF GROUND-ACTIVE LIZARDS IN PITFALL TRAPS

Abstract

Pitfall traps are commonly used to capture terrestrial vertebrates and invertebrates, but it is not known whether differences in vegetation structure affect the efficiency of these traps. Many studies use capture data from pitfall traps to compare areas with different vegetation structures. For example, there are numerous studies comparing faunal communities in different habitats, areas with different fire history, and more recently, areas with different levels of grazing by domestic stock. These studies are potentially confounded by differences in the efficiency of the trapping technique between the areas being compared; hence, the validity of using pitfall traps to sample populations under these circumstances should be determined. This study tests the hypothesis that reducing the cover of ground vegetation affects the rate at which lizards are captured in pitfall traps.

The study was undertaken in an area of mulga (Acacia aneura) tall shrubland in central Australia. Grasses and forbs were cut in three of six, 30 m by 30 m, field enclosures, to emulate the effect of cattle grazing on the structure of ground vegetation. Plant cover was reduced from approximately 27% to 10%. Pitfall traps were used to capture lizards in all enclosures before and after grass was cut. Reducing the cover of ground vegetation had no effect on the subsequent rates at which lizards were captured, compared with the three control enclosures, or rates of capture before grass was cut. The rate of capture of one species was significantly lower in all enclosures after the experimental manipulation, but this was not related to cutting grass and was probably a response to changes in temperature and other climatic conditions during the study. I conclude that within the range of vegetation covers used in this study pitfall trapping is a valid technique for comparing lizard populations in mulga shrublands which are subject to different levels of grazing.
Introduction

The success of pitfall trapping is affected by the behavior and activity of animals because it is a passive technique. High levels of surface activity, defined here as the total horizontal distance moved by an animal over a fixed period, increase the likelihood of an animal encountering a trap and so result in a greater number of captures. For example, surface active species are obviously more likely to be captured in pitfall traps than arboreal species. Only a sub-set of the species present at a site are effectively sampled by pitfall traps and the relative abundance of species among captures does not necessarily correspond with the relative abundance of species in the area being sampled. Similarly, behavioral differences within a species, for example between males and females (Rose 1981; Kingsbury 1989), or at different stages in the reproductive cycle (Rose 1981), can affect the susceptibility of sub-sets of a species to capture in pitfall traps.

Population models applied to mark-recapture data can be used to estimate the abundance of individual species in some circumstances. However, if the proportion of the population that is marked is very small, or the number of subsequent recaptures is low, population estimates will not be accurate (Caughley 1977). Under these circumstances it is difficult to correctly interpret the relationship between capture data and abundance. However, knowledge of comparative abundance of different species may not always be crucial. For example, an index of abundance, derived from the number of captures in pitfall traps, can be an appropriate measure for comparing the abundances of a single species at different sites. Provided that the limitations of the technique are recognised, pitfall trapping can be a practical and efficient method for investigating populations of small, terrestrial lizards.

The limitations of using data from pitfall traps for estimating species diversity and abundance of lizards are widely recognised (e.g. Mather 1979; Fye 1980; Longmore & Lee 1981; James 1994). The complications with interpreting data from pitfall traps have also been discussed in the literature on invertebrates (e.g. Greenslade 1964; Hayes 1970; Marsh 1984; Halsall & Wratten 1988; Andersen 1991; Topping & Sunderland 1992). Studies designed to test how effective pitfall trapping is for capturing invertebrates have usually compared the number of captures in pitfall traps with other methods of capture (Hayes 1970; Andersen 1991; Olson 1991; Topping & Sunderland 1992). A few studies have compared the relative efficiencies of different pitfall trap designs for capturing vertebrates (e.g. Braithwaite 1983; Friend 1984; Morton et al. 1988, Friend et al. 1989; Hobbs et al. 1994).
One question which has remained unexplored is whether pitfall traps are equally efficient in capturing reptiles in areas with dissimilar vegetation structure. This question is of paramount importance because in many studies vegetation structure differs, almost by definition, between sites being compared. In studies which compare different habitats, or habitats that have been altered by fire or grazing, the response of fauna to differences in vegetation structure is often integral to the question being addressed. If the efficiency of the trapping technique varies according to vegetation structure, this will directly confound the effect under investigation. However, this problem is rarely recognised or discussed in such studies.

My aim was to address the question of whether vegetation cover affects the rate at which lizards are captured in pitfall traps in the context of comparing lizard assemblages at sites with different grazing levels. Pitfall trapping was the sole technique used to capture lizards in the grazing study which is the primary subject of this thesis. Estimates of vegetation cover at each of the sites confirmed that mean vegetation cover at ground level was generally lower at sites with high levels of grazing, although there was considerable variation in cover among sites within each level of grazing (Chapter 2). A change in the structure of vegetation is one of the mechanisms by which cattle grazing may affect lizard populations, and I found direct correlations between the abundance of some lizard species and vegetation structure (Chapter 2). Considering these factors, there was a serious potential for misinterpreting data for the relative abundance of lizards at sites with different grazing levels if the efficiency of pitfall traps in capturing lizards differed according to vegetation cover. Therefore, the specific objective of the experiment reported in this chapter was to assess whether pitfall traps were equally efficient in capturing lizards at sites which had different levels of grazing by cattle in mulga shrublands in central Australia (see Chapter 2).

I designed the experiment to enable detection of short-term changes in the rates of capture of lizards in response to a reduction in the cover of ground vegetation. The experiment was conducted in field enclosures so that lizards could not move into or out of areas with reduced ground cover, and differences in vegetation cover were intended to be directly comparable to those between sites with different levels of grazing (Chapters 2 & 4). I tested the hypothesis that the number of lizards captured in pitfall traps, from a fixed population, over a short period of time, differs at sites where the cover of ground vegetation has been artificially reduced.
Methods

The experiment was conducted on Hamilton Downs Station, approximately 60 km north-west of Alice Springs in central Australia. Vegetation in the area was dominated by groved mulga (*Acacia aneura*) shrubland (Lendon & Ross 1978) with a mixture of perennial and annual grasses and forbs dominating the understorey. Dominant species were woollybutt grass (*Eragrostis eriopoda*), windmill grass (*Enteropogon acicularis*) and the annual grass *Aristida contorta*. The experimental site was more than 6 km away from the nearest watering point for stock, at a distance where grazing impact is low (Pickup & Chewings 1988).

I constructed six adjacent field enclosures, measuring 30 m by 30 m. Three enclosures were chosen randomly as treatment plots in which grass would be cut, and three as control plots. Four trap units, each consisting of two 20 l pits joined by 10 m of drift fencing, were installed in each enclosure (Figure 3.1). I chose an area containing relatively few trees so that, aside from differences in ground cover, vegetation in each enclosure was similar.

The walls of the enclosures were made from 2 mm thick black plastic which was suspended from wire strung between star pickets. I hung the plastic from the wire and secured it with wooden clothes pegs, in combination with staples, because this method of attachment allowed for the expansion and contraction of the plastic in response to daily temperature changes. The plastic fences were 65 cm high and were buried approximately 20 cm beneath the ground to prevent lizards from burrowing underneath. I also installed a single strand of electric fence 30 cm above the plastic to prevent stock from entering the enclosed areas and damaging the fences.

Enclosures were built during late winter 1995 and trapping commenced in late September to coincide with the early reproductive season. This was also a time of year when lizards were least likely to be thermally stressed and when I anticipated that temperature dependent variation in the level of activity on different days would be minimal compared to other times of the year. I initially opened the traps for thirty days (26th September - 20th October and 3rd - 9th November) to determine whether there were any pre-existing differences in the number of lizards or the rate of capture among enclosures. Trapped lizards were measured, weighed and given a unique toe-clip for future identification. Very few unmarked animals were captured toward the end of the initial trapping period, which suggested that the majority of active animals confined within the enclosures had been successfully trapped.
Figure 3.1 The physical layout of field enclosures and pitfall trap units and the relative position of treatment and control enclosures.
After the initial trapping period I cut vegetation in the three treatment sites, with a petrol powered, hand held, grass cutter, to simulate the effect of cattle grazing. All grass clumps of significant size were cut to a height of approximately 2 cm. After grass was cut I raked each enclosure to remove as much of the new grass litter as possible, although this was sometimes difficult because the pieces of grass were small. I also raked the control sites, without actually removing any material, in order to simulate the disturbance.

I recommenced trapping five days after grass was cut. This delay was a compromise between allowing any immediate effects of the disturbance to subside and minimising seasonal effects on lizard activity. Trapping after treatment was continuous, for a total of thirty-five days (15th November - 20th December).

Mean cover of ground vegetation in each enclosure was measured along three, 30 m transects before and after the manipulation to derive a quantitative measure of the change in vegetation cover which resulted from cutting grass. A tape measure was placed along each of the transects and the lengths over which the tape intersected with vegetation or leaf and grass litter were recorded and subsequently converted to estimates of percentage cover.

Results

General results

Eleven species and a total of 200 lizards, including 154 marked recaptures, and one snake were captured in the enclosures (Table 3.1).

There were a few occasions when lizards were captured in an enclosure adjacent to the one in which they were originally found, which suggested that fences were not an impenetrable barrier to lizards. This was probably a result of occasional tears in the plastic which were repaired as soon as they were discovered. Recapture data suggested that this movement was uncommon and not biased with respect to cut and uncut treatments: five lizards moved out of cut enclosures and three lizards moved out of uncut enclosures out of a total of 154 recaptures. It is unlikely that these movements affected my results.

Treatment effect on cover and litter

Initially, average ground cover across all enclosures was 27% (SD = 4). The average cover of ground vegetation in treatment sites after cutting was 10% (SD = 2), and the average difference in cover between treatment and control sites was 19.8% ($t_{ad} = 8.43$, 42
Table 3.1 Species and numbers of reptiles captured in field enclosures over 65 days of trapping.

<table>
<thead>
<tr>
<th>Species</th>
<th>First captures</th>
<th>Recaptures</th>
</tr>
</thead>
<tbody>
<tr>
<td>GEKKONIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplodactylus conspicillatus</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td>Diplodactylus stenodactylus</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Gehyra variegata</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Rhynchoedura ornata</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>PYGOPODIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pygopus nigriceps</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>AGAMIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lophognathus gilberti</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Pogona vitticeps</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>SCINCIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenotus leonhardii</td>
<td>50</td>
<td>62</td>
</tr>
<tr>
<td>Ctenotus schomburgkii</td>
<td>53</td>
<td>59</td>
</tr>
<tr>
<td>Menetia greyii</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>ELAPIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suta punctata</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>146</strong></td>
<td><strong>154</strong></td>
</tr>
</tbody>
</table>
The percentage cover of litter in treatment sites was not significantly different from that before cutting ($t_{df} = 2.07, P = 0.18$).

**Treatment effect on lizard captures**

Only two species, *Ctenotus leonhardii* and *Ctenotus schomburgkii*, were captured in sufficient numbers to enable independent analysis. Data for gecko species, except the only arboreal species, *Gehyra variegata*, were pooled. The remaining geckos are terrestrial, nocturnal and of similar size, and so might be expected to have a similar response to changes in habitat structure.

Both original captures and recaptures were used in analyses. Data for each species or group, before and after cutting grass, in each enclosure were standardised to capture rate per day and log transformed prior to analyses.

I used repeated measures analysis of variance to compare capture rates before and after cutting grass and in treatment and control enclosures. This analysis enabled a simultaneous test of differences in capture rate between treatment and control enclosures after cutting grass and for possible pre-existing differences between these enclosures.

Cutting the grass did not affect the rate of capture of either of the *Ctenotus* species or of the geckos (Figure 3.2). That is, there was no significant interaction between treatment and time (*C. leonhardii*: $F_{1,4} = 0.62, P = 0.48$, *C. schomburgkii*: $F_{1,4} = 3.87, P = 0.12$, geckos: $F_{1,4} = 0.59, P = 0.48$). There was an effect of time on the number of *C. schomburgkii* captures, with fewer animals being captured during the second part of the experiment ($F_{1,4} = 25.17, P = 0.006$), but this pattern occurred in both treatment and control enclosures (Figure 3.2). Data for the infrequently captured species not included in previous analyses were pooled in a separate analysis and no effect of cutting grass on capture rates was detected ($F_{1,4} = 0.04, P = 0.85$). The number of species captured in treatment and control enclosures also did not differ in response to the cutting of grass ($F_{1,4} = 1.56, P = 0.28$).

Daily capture rates of all species combined were examined to determine whether there were any obvious differences in the daily variation in captures between treatment and control enclosures after cutting grass. Such differences may be obscured when only total captures over a period of time are considered. Capture rates and daily temperatures are shown in Figure 3.3. There was an obvious correspondence between mean daily capture rates in treatment and control enclosures with peaks and lows in the number of captures occurring on the same days (see Figure 3.3). This pattern suggests that daily activity at these sites had a non-random component which was
Figure 3.2 Mean rate of capture of *Ctenotus leonhardii*, *Ctenotus schomburgkii* and geckos before and after grass was cut in treatment enclosures (open circles) and control enclosures (closed circles). Error bars are standard errors.
Figure 3.3 Mean number of lizards captured per day in treatment and control enclosures and daily minimum and maximum temperatures over the period during which trapping took place.
probably due to weather conditions. The correspondence is most obvious during the early part of the study, before and on the days immediately after grass was cut. Toward the end of the study, capture rates were particularly low and random noise in the data may have obscured any patterns. There is some correspondence between daily temperatures and the number of captures (Figure 3.3) but direct correlations between temperature and activity were not significant. The relationship between temperature and capture rates is complex; for example, after grass was cut the number of captures did not increase despite a gradual increase in daily temperatures. However, there appeared to be a positive relationship between the rate of capture and daily minimum and maximum temperatures during the first weeks of trapping. No differences were apparent in the daily variation in the rate of capture of lizards between treatment and control enclosures.

Discussion

Cutting grass in the three treatment enclosures had no effect on the subsequent rate of capture of *Ctenotus leonhardii, Ctenotus schomburgkii* or geckos, so it is also unlikely that differences in vegetation cover among sites in the grazing study affected the efficiency of pitfall-trapping for capturing these species. Cover of ground vegetation was measured twice during the grazing study. Differences in cover between heavily and lightly grazed sites were only significant in June 1995, after a wet period (Chapter 6); mean ground cover at sites with high levels of grazing was 10.5% and at low levels of grazing was 15.2%. The highest and lowest covers measured at any site or time during the study were 4.1% and 17.6% (Chapter 6). Ground cover was reduced by 14.5% in the manipulative experiment described in the present chapter, a figure far exceeding the differences in mean cover between sites with high and low levels of grazing, but of similar magnitude to that between the sites with highest and lowest cover. If differences in ground cover between sites in the grazing study affected the efficiency of the trapping technique, an effect of the experimental manipulation of ground cover on rates of capture should also have been detectable. Hence, any differences in the number of lizards captured at the sites in the grazing study should reflect real differences in relative abundance, or differences in activity, which do not relate directly to the efficiency of the trapping mechanism.

In central Australia, the activity of lizards varies considerably over time (Chapter 4). In general, there is a positive relationship between the number of captures and daily temperature in spring and autumn but activity seems to be independent of daily temperature in summer (Chapter 4 and unpublished data from this study). The manipulative experiment described here was planned to span a period during which daily fluctuations in temperature were least likely to affect the activity of lizards;
however, the gradual increase in temperatures during the trapping period (Figure 3.3) may have affected the level of activity of some species. The increase in temperature may explain why mean captures in treatment and control enclosures appeared to be synchronous during the first part of the study and immediately after grass was cut (when there was a positive relationship between temperature and activity), and why this synchrony became less obvious as trapping proceeded (Figure 3.3). Capture rates were also lower toward the end of the experimental period, so patterns were harder to detect at this time. Nevertheless, there was no evidence that the relationship between temperature and capture rates, or the variation in capture rates in general, differed between treatment and control enclosures after grass was cut. The significant difference in the number of captures of *C. schomburgkii* before and after the manipulation illustrates the importance of having data for both treatment and control sites, before and after the treatment is applied, for studies in temporally variable environments (Osenberg *et al.* 1994). The lower abundance of *C. schomburgkii* in treatment enclosures may have been interpreted as an effect of cutting grass if capture rates in control sites had not been shown to follow a similar trend.

Apart from the low capture rates, particularly after grass was cut, there were certain other limitations of this study. It is possible that confining lizards within enclosures may have affected their behavior during the experiment. Drift fences and enclosure fences may also have obstructed lizard movement or provided alternative shelter opportunities for lizards, thus reducing the impact of cutting grass. Finally, the results of this study cannot be extrapolated to other species or other environments or necessarily to other times of the year when interactions between temperature, vegetation cover and lizard activity may differ. The temperatures during this experiment were, however, broadly representative of temperatures in spring, summer and autumn in central Australia, so it is likely that results would have been the same throughout the active season for lizards.

Aside from these limitations, this study has clearly indicated that reducing ground cover did not affect the rate at which lizards were captured. My result is in contrast to the findings of some previous studies of the effect of vegetation structure on the activity of invertebrates. For example, Crist *et al.* (1992) tracked the movement of *Elodeas* beetles in areas with different cover types and grazing intensities and found that net displacement was greatest on open ground. Honek (1988) found that the total number of carabid beetles caught was greater in sparse stands of vegetation than in dense stands, although this result may also have been due to changes in the density of beetles. Two studies have specifically tested whether vegetation density affects the efficiency of pitfall traps. Greenslade (1964) noted that traps were slightly more efficient for capturing carabids in areas with sparse ground cover compared with more
densely vegetated areas; Melbourne (1993) found a similar effect on the rate of capture of some ants and crickets. In both these studies, however, replicate plots were not enclosed and vegetation manipulations were restricted to a small area immediately surrounding the traps (60 cm and 80 cm in diameter in Greenslade (1964) and Melbourne (1993) respectively). Hence, there was no knowledge about the number of animals able to access each trap, and it remains uncertain whether the species caught in higher numbers in sparsely vegetated sites were attracted to these areas, or whether activity levels were higher within the area.

In my study, I sought to isolate differences in the rate of capture of lizards which related specifically to the efficiency of pitfall-trapping from changes in abundance or behavioral responses to reduced cover which may ultimately affect the abundance or health of populations. Table 3.2 lists a number of factors which affect the abundance and activity of lizards. Hypothetically, differences in ground cover in the grazing study may have affected each of these factors and, consequently, the number of lizards captured in pitfall traps. In the experiment described in this chapter, I constructed enclosures to ensure that capture rates were not affected by immigration, emigration or changes in home range. By conducting the experiment over a short period of time in spring and summer I also reduced the possibility that natality or mortality would affect abundance, and I also attempted to limit any effect of grass-cutting on the thermal environment or on prey abundance. Although grass-cutting may have affected the rate of mortality of lizards as well as the abundance of prey species - the barriers used to enclose lizards would not have been impenetrable for many invertebrates - any short-term effects on lizard captures relating to these factors would have differed from longer term effects at sites used in the grazing study. Although the thermal environment was altered by cutting grass, I attempted to limit the effect of these changes on the behavior of lizards during the experiment by avoiding seasons when temperatures were extremely high or low.

Primarily, therefore, the experiment tested whether the last two factors in Table 3.2, physical obstruction of movement and activity levels or search time relating to habitat complexity, changed when ground cover was reduced. The result of the experiment, that rates of capture of lizards did not differ between cut and uncut enclosures, indicates that differences in the obstruction of movement or search time did not affect capture rates. It also indicates that, in the short term, rates of mortality did not change, and any changes in the thermal environment or in prey abundance did not affect activity. More importantly, the results are evidence that any differences in numbers of lizards captured in the grazing study, which reflect differences both in activity and abundance, do not reflect differences in the efficiency of pitfall-trapping.
Table 3.2 Factors that affect the abundance and activity of lizards which could be altered by changes in vegetation structure. Those factors which may have affected the number of lizards captured in the experimental study and the grazing study are indicated. An asterisk indicates that the factor may have been altered by cutting grass but that effects on lizard captures in the experiment are expected to be limited compared to those in the grazing study. Primarily, the experiment tested whether cutting grass affected those aspects of activity in the boxed area of the table.

<table>
<thead>
<tr>
<th>Factors that influence lizard activity and abundance that may be affected by the cover of ground vegetation</th>
<th>Potential effect on no. captures in experiment</th>
<th>Potential effect on no. captures in grazing study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>• immigration and emigration</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>• natality</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>• mortality</td>
<td>No*</td>
</tr>
<tr>
<td>Activity</td>
<td>• thermal environment</td>
<td>No*</td>
</tr>
<tr>
<td></td>
<td>• home range size</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>• prey abundance and required foraging effort</td>
<td>No*</td>
</tr>
<tr>
<td></td>
<td>• physical obstruction of movement</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>• the effect of habitat complexity on the time required to search for food</td>
<td>Yes</td>
</tr>
</tbody>
</table>
Ground cover in central Australian mulga shrublands is relatively low in comparison with the invertebrate studies which I have reviewed above. In combination with differences in mobility between lizards and ground dwelling invertebrates, this difference may further explain the disparity between my results and the results of other studies. Melbourne's (1993) experimental plots ranged from dense grassland to completely bare ground. Greenslade (1964) also cleared all vegetation at bare sites and dense vegetation sites consisted of a dense "mat". Honek (1988) compared captures of Coleoptera and Araneae on bare ground with sparse and dense stands of winter wheat. Crist et al. (1992) studied distances moved by beetles in heterogeneous landscapes, and all sites had a matrix of grass cover greater than 50%. Clearly, all these studies were conducted in vegetation which was originally much denser than the mulga sites of this study, and the differences in cover being compared were more extreme. Additionally, the cover in the mulga sites was very patchy, with ample open ground available in all enclosures. Whereas the studies mentioned above suggest that dense vegetation obstructs the movement of invertebrates, the typically sparse vegetation cover in the mulga habitat apparently presents little obstruction to lizard activity.

In conclusion, the results presented in this chapter suggest that the efficiency of pitfall traps in capturing lizards is not affected by differences in ground cover in arid mulga shrublands. Hence, differences in capture rates between heavily and lightly grazed sites appear likely to reflect actual differences in abundance or differences in activity rather than being related to the trapping process.
Chapter 4

Temporal variation in lizard activity and abundance on pastoral land in central Australia: The effect of rainfall and temperature
Chapter 4: Temporal variation in lizard activity and abundance

TEMPORAL VARIATION IN LIZARD ACTIVITY AND ABUNDANCE ON PASTORAL LAND IN CENTRAL AUSTRALIA: THE EFFECT OF RAINFALL AND TEMPERATURE

Abstract

The activity and abundance of lizards in the central Australian arid zone varies considerably through time in response to highly irregular and unpredictable rainfall, and seasonal variation in temperature. Temporal patterns of activity of six lizard species were assessed in relation to climatic conditions, plant growth and invertebrate biomass, and the abundance of each species at sites with different levels of grazing was compared. The study was conducted between September 1993 and December 1995 in mulga (Acacia aneura) shrubland within a pastoral property. Sites were categorised as having high or low levels of grazing based on their distance from watering points provided for cattle.

The timing of activity in different years was variable and did not correspond closely to seasons, except for geckos. The diurnal lizards, two skinks (Ctenotus leonhardii and Ctenotus schomburgkii) and the agamid (Ctenophorus nuchalis), delayed spring activity after a long dry period, which coincided with low rates of plant growth, but maintained high levels of activity in the following autumn and winter. In contrast, the activity of geckos was consistently correlated with temperature, and activity was generally restricted to the warmer months of each year. Correlations between lizard activity and environmental variables differed at different time scales and according to when each species was active in a particular year.

Ctenophorus nuchalis occurred almost exclusively at sites with high levels of grazing and increased in abundance toward the end of the study. There were no significant differences in the abundance of geckos between sites with different levels of grazing at any time. Two skink species, Ctenotus leonhardii and Ctenotus schomburgkii, were generally more abundant at sites with low grazing levels but this trend was not consistent at different times. Differences in lizard abundance between sites with high and low levels of grazing were least apparent in the year when activity was delayed. The effect of differences in vegetation cover associated with grazing level on the availability of thermal microhabitats is likely to be much greater for diurnal lizards than for nocturnal species. Because Ctenophorus nuchalis is tolerant of extremely high temperatures and prefers open habitats, it may be able to exploit areas with low cover of vegetation such as occur at sites with high levels of grazing. However, high exposure at these sites may limit the activity of Ctenotus under certain circumstances. This may explain why skinks were less abundant at sites with high levels of grazing at some times but not at others.
Introduction

Moisture input is the primary factor limiting productivity in desert ecosystems. Australian deserts have relatively high mean annual rainfall (≈ 270 mm in the Alice Springs region in central Australia) but the timing of rainfall is highly variable and unpredictable compared to other desert systems in the world. Annual rainfall totals are skewed towards lower values with the median annual rainfall in Alice Springs, calculated from 114 years of records, being only 236 mm. The minimum and maximum annual rainfalls recorded in Alice Springs are 60 mm and 782 mm respectively (data from Bureau of Meteorology). The timing of rainfall within a year is also highly variable in the region. Many rainfalls are too small to significantly affect plant growth (Williams & Calaby 1985) and, at the other end of the spectrum, large rainfalls, which play an important role in structuring both physical and biotic environments, only occur occasionally and at irregular intervals. For example, an extremely large rainfall event in 1988 resulted in 80% of the mean annual rainfall occurring in 24 h (Stafford Smith & Morton 1990). Predictably, populations of native fauna fluctuate dramatically in response to this temporal stochasticity in rainfall and productivity.

Mulga shrublands (dominated by Acacia aneura) are one of the most extensive vegetation associations currently used for pastoralism in semi-arid and arid Australia. Unlike the native fauna, which have adapted to live and breed successfully under conditions where rainfall is unpredictable and surface water is not readily available, domestic cattle and sheep depend on the availability of drinking water to survive. In the early days of pastoralism in the region, productive patches of land, particularly those with permanent or temporary natural water sources, were the predominant focus for grazing (Morton et al. 1995). Large areas of mulga shrubland were inhospitable for livestock during dry periods because of the scarcity of surface water and stock could only be moved to these areas during occasional periods of high rainfall. The discovery of ground water, and the development of technology to access this resource, led to the installation of artificial water sources which enabled cattle to be moved permanently on to the relatively infertile mulga plains. The land surrounding these water points became a new focus of grazing activity.

There is currently little information about the impact of pastoralism on faunal groups (see James et al. in press for a review), particularly for reptiles. The data that are available suggest lizard abundance may decrease in areas that are heavily grazed (Busack & Bury 1974; Jones 1981; Bock et al. 1990). The effect of grazing on vegetation cover (e.g. see Pickup et al. 1993; Bastin et al. 1993; Bastin et al. 1996), as
well as possible changes in the abundance of invertebrates, is the most likely way in which grazing might affect the abundance of lizards in arid Australia (Morton et al. 1996).

Strong links between structural characteristics of habitats and the distribution and abundance of lizards have been demonstrated in numerous studies, and in an environment in which temperatures are often extreme, vegetation structure may be very important in providing shelter, or a range of suitable thermal microhabitats, for diurnal lizards (Chapter 2, Morton et al. 1996). I have already reported that diurnal skinks were more abundant at sites with low levels of grazing, compared to more heavily grazed sites in mulga shrubland, and that the diurnal agamid, *Ctenophorus nuchalis*, was far more abundant at sites with high levels of grazing (Chapter 2). In contrast, the abundance of geckos, which are all nocturnal, did not differ at sites with different grazing levels (Chapter 2). Differences in vegetation structure, which affect the thermal environment, may be more important for diurnal lizards. However, the interactions between habitat structure, the thermal environment, and temporal patterns of lizard activity and their use of space are complex and variable through time.

The effect of grazing on vegetation structure is itself dynamic. For example vegetation can recover substantially from the impacts of grazing after periods of rain. If grazing affects vegetation structure to varying degrees in space and time, and vegetation structure is important in defining the thermal environment available to lizards (to varying degrees depending on season and on the habits of different species), it follows that the effect of grazing on lizards will not be the same at different times. In central Australia, the possible impacts of grazing on lizard communities cannot be adequately assessed without taking into account the over-riding effect of climatic conditions on temporal fluctuations in lizard activity and abundance, and the possible interactions between habitat disturbance and climate variability.

Although there is little specific information on temporal fluctuations of lizard populations in Australian mulga shrublands, there is an abundance of published documentation of relationships between climatic variables, plant growth, invertebrate abundance and reptile activity and abundance in other habitats. Fluctuations in the activity of reptiles are most commonly attributed to temperature (e.g. Bradshaw 1986; Pianka 1986; Heatwole & Taylor 1987) and rainfall (James 1991a; Smith et al. 1995), photoperiod (Licht 1973) and prey abundance (e.g. Ballinger 1977; Whitford & Creusere 1977; Schoener & Schoener 1978), but relationships have also been documented with many other variables such as humidity (Diaz-Paniagua et al. 1995) and moon phase (Houston & Shine 1994). In desert systems, temperature and rainfall are considered to be the primary components of climate which affect temporal

The main pathways by which temperature and rainfall may contribute to patterns of lizard activity in central Australia, based on current knowledge, can be summarised in a simple conceptual model (Figure 4.1). In central Australia there is an abundance of warm, clear days which are suitable for lizard activity. Nevertheless, winters can be cool (in July average Tmin = 4°C, average Tmax = 19°C) and in summer daily maximum temperatures are frequently above 40°C. Therefore changes in temperature during the year and within each day potentially have a significant effect on the activity of ectothermic animals. Consequently, I have linked temperature directly with lizard activity and invertebrate biomass in the model (Figure 4.1). Temperature also interacts with rainfall to stimulate herbage growth as well as directly affecting herbage growth and decay irrespective of rainfall, as indicated in the model. Many invertebrate species respond directly to climatic conditions and plant growth (Cloudsley-Thompson 1991) and, in turn, predatory invertebrates and lizards are expected to respond to fluctuations in the abundance of their prey. Rainfall is also linked directly with invertebrate biomass and lizard activity in the model (Figure 4.1) because rainfall can directly stimulate (or inhibit) activity. However, because there are so few rain days in a year, I predict that the link between rainfall, plant growth and invertebrate abundance, is more important in determining activity patterns of lizards than any direct effect of rainfall on daily activity (see Figure 4.1).

I sampled terrestrial lizard assemblages in mulga shrublands over a period of 27 months at sites with different levels of grazing so that temporal patterns of activity and abundance of different species could be assessed, and to determine whether the relative abundance of lizards at sites with different grazing levels was consistent over this period. I use the model (Figure 4.1) as the basis for exploring relationships between environmental variables and lizard abundance at sites with different levels of grazing, and to determine which variables are the best predictors of lizard activity and abundance at different time scales.

Six species of lizard, belonging to three families with distinctly different habitat requirements, foraging modes and daily activity cycles, were examined with the following specific objectives.

1. Fluctuations in activity and abundance through time were investigated to:
   a) identify seasonal distributions of activity within years and determine whether these patterns were consistent in different years;
   b) compare the temporal distribution of activity in different species;
Chapter 4: Temporal variation in lizard activity and abundance

Figure 4.1 Model of predicted pathways by which temperature and rainfall may influence the activity of lizards through time. Solid lines indicate strong functional relationships and dashed lines indicate weaker relationships which may be important at some times.
c) compare the temporal distribution of activity at sites with different levels of grazing; 
d) identify appropriate time scales for comparisons of the abundance of species at sites 
with different grazing levels and assess whether differences occur during these times.

2. The relationship between patterns of activity and abundance of different species with 
temperature, rainfall, plant growth and invertebrate abundance were examined: 
a) in different seasons, to determine whether the number of lizards captured in a 
particular season can be linked to particular climate variables; and 
b) over time frames relating to different stages of the yearly activity cycles of lizards, to 
determine whether the relationship between lizard activity and environmental variables 
varied according to the stage of activity, grazing level, or the timing of activity in a 
particular year.

3. For each species, the implications of the temporal and spatial variation of 
populations and correlations with environmental variables were interpreted in the 
context of the effects of grazing.

Methods

Study sites and procedure for sampling lizards

Study sites were located on a cattle property north-west of Alice Springs, in low open 
shrubland dominated by mulga (Acacia aneura). Eight sites were chosen based on 
their proximity to artificial water points (see Chapter 3 for detailed information on site 
selection). Four sites were less than 1 km from a water point and had been 
consistently used by cattle for many years, probably since the 1930s and 1940s when 
the majority of wells and bores were developed on the property (Low 1978), and were 
in use throughout the study. Four sites were more than 6 km from the closest 
permanent water. Cattle infrequently graze at this distance from water in mulga (Low 
et al. 1973). The intensity of grazing at the sites close to water varied, both during this 
study and historically, depending on stocking rates in each paddock, weather 
conditions, and the exact time each water point was developed. These differences in 
grazing intensity among sites at a particular distance from water are not considered 
here. This study was designed to investigate temporal fluctuations in lizard activity 
and how these relate to environmental variables and to determine whether there are any 
generic changes in lizard populations relating to these factors which have resulted from 
a long history of grazing and are detectable against the underlying heterogeneity in the 
landscape.

Each of the eight sites had 40 pit traps, arranged in pairs, joined by drift fences. 
Trapping methods and the lay-out of pitfall traps are fully described in Chapter 3.
Terrestrial lizard assemblages at each site were sampled at monthly intervals between October 1993 and December 1995 so that temporal and spatial patterns of variation could be quantified over different time periods. Drift fences were left in place throughout the study (Chapter 2). The possibility that this may have caused animals to adjust their home ranges and avoid traps altogether was weighed against the disturbance and time taken to collapse and re-erect each fence between trips. Based on the short duration and high frequency of trapping periods, I decided to leave the fences in place. It was not possible to trap simultaneously at all eight sites because of the distance between sites and the time required to check traps. Consequently, half of the traps were opened at a time, resulting in two trapping periods each month. Traps at the same four sites (H1, L1, H2, L2 and H3, L3, H4, L4) were always opened together and consisted of two sites close to a water point, with high levels of grazing (prefix H) and two sites far from a water point, with low levels of grazing (prefix L). Heavy rain caused flooding on access roads in December 1993, February 1994 and January 1995. Some sites were still accessible in February 1994, but no data were collected during the other two months. Hence data were collected in 25 months over a 27 month period.

During the first two months of trapping, several animals were killed by over heating as a result of exposure to direct sunlight. This problem was alleviated by leaning the lids of the pails against the fence above each pit, thus providing shade for captured animals throughout the day. This method of shelter did not appear to adversely affect capture rates and was used throughout the rest of the study. However, the rate of capture during the first two months of trapping should only be compared with the rest of the study with caution, because the efficiency of the trapping method may have differed slightly during this time. Comparisons between sites are valid, because the trapping method was consistent across all sites at all times.

Temporal and spatial patterns in activity and abundance of six species are examined: the central netted dragon (*Ctenophorus nuchalis*), two skinks (*Ctenotus leonhardii* and *Ctenotus schomburgkii*) and three geckos (*Diplodactylus conspicillatus*, *Diplodactylus stenodactylus* and *Rhynchoedura ornata*). *Ctenophorus nuchalis* is a diurnal, ambush predator which typically occurs in open areas and is often exposed to, and tolerant of, extremely high temperatures (Heatwole 1970). The two species of skink are small, active, diurnal lizards. The three species of geckos are nocturnal, ground-dwelling lizards which occupy burrows.
Patterns of activity and abundance over time

For all comparisons of activity and abundance between years, each year is defined as beginning in spring (September-November) and continuing through summer (December-February), autumn (March-May) and winter (June-August). The climate of central Australia is characterised by hot summers and cool winters. Temperatures often fluctuate dramatically in spring and autumn. Hence a seasonal breakdown of data represents four periods during which the temperatures defining the thermal environment available to lizards are distinctly different. Data were initially categorised according to seasons to investigate patterns of activity and abundance of lizards over the entire period of the study and to determine whether the seasonal distribution of activity was consistent between years.

For each season (spring, summer, autumn and winter) the average of the three samples at each site, one in each month, was calculated to represent the rate of capture in that season (in some seasons only one or two months data were available). Because these averages were derived from temporally replicated data, usually six random periods within each season, the resulting estimates of capture rates for each season are unlikely to be confounded by fluctuations in lizard abundance or activity over shorter time scales. Data were log transformed prior to all analyses. Repeated measures analyses of variance were used to test the following null hypotheses: (a) that the relative abundance of lizards in different seasons did not differ among years; and (b) that the relative abundance of lizards at sites with different grazing levels did not differ among years or seasons. Years and seasons were the two repeated factors in the analyses and level of grazing was the between factor. Two analyses were performed for each species to overcome problems with unbalanced representation of seasons in each year. In the first analysis, captures in four seasons were compared over the first two years of the study. A second analysis was performed on data collected over three years, in spring and summer only, as data for autumn and winter were not collected in the third year. This analysis provided a stronger comparison between years than the analysis which used data for all seasons.

For each species, the number of captures in each month were plotted to enable interpretation of the results of the analyses described above and to further examine temporal patterns of activity on a monthly scale. The number of captures at heavily and lightly grazed sites were plotted separately and the synchrony of peaks and lows of activity in these sites was assessed visually. Adult and juvenile data were also plotted separately to provide an insight into the underlying dynamics of each population.
Chapter 4: Temporal variation in lizard activity and abundance

Adults and juveniles were distinguished by their snout-vent lengths. Snout-vent length at maturity was estimated to be 74% of the maximum snout-vent length for each species. This relationship is widely applicable to lizards in North America over several familial groups (Shine & Charnov 1992). The estimates of snout-vent length at maturity derived from this relationship corresponded well with published data for the two *Ctenotus* species (James 1991b); however, data from Bradshaw (1981) indicated that *Ctenophorus nuchalis* reach maturity at a significantly lower snout-vent length than the estimated value of 74% of maximum snout-vent length. Bradshaw’s (1981) recorded value (67 mm) was used to define maturity for this species. Independent data were not available for the gecko species but I have assumed that maturity was reached at 74% of snout-vent length for this group. Lizards that were identified as having reached sexual maturity, based on their snout-vent lengths, were categorised as adults and all other individuals were considered to be juveniles.

*Redefinition of time scales*

Because the timing of activity varied considerably between years (see Results), periods which corresponded with months when activity was highest were identified as a more appropriate temporal category than calendar seasons for further analyses. For adults, months of peak activity were identified, as well as the months of moderate activity immediately prior to (early activity) and immediately following (late activity) peak months. For juveniles the months when the emergence of new hatchlings was highest (emergence) and the months following this (post-emergence) were identified. The months when sub-adult lizards were active (sub-adults), after winter but before any new hatchlings appeared, were also identified.

*Abundance of lizards at sites with different grazing levels during periods of peak activity*

Mean rates of capture, at each site, were calculated for each of the defined activity periods. The null hypothesis that abundance of lizards at sites with different grazing levels did not differ during months of peak activity was tested separately in each year with a series of unpaired t-tests. For *Ctenotus leonhardii* and *C. schomburgkii* differences in the number of newly emerged juveniles at sites with different grazing levels were also assessed in each year.
Correlations between lizard activity and environmental variables

Environmental variables

The environmental variables considered as possible correlates to the abundance of lizards were maximum and minimum temperature (Tmax & Tmin), herbage growth, herbage biomass and invertebrate biomass.

It is difficult to identify quantitative relationships between lizard abundance and rainfall over short time periods, for example within a month, when rainfall occurs very infrequently. I did not test for direct relationships between rainfall and lizard abundance. Estimates of herbage growth and biomass derived from rainfall data were used, as an alternative to lag periods relating to rainfall, to investigate a possible mechanism by which rainfall interacts with other environmental variables to produce conditions that might ultimately influence the abundance and activity of lizards.

Climate data for the Alice Springs region and rainfall data for Hamilton Downs Station were obtained from the Bureau of Meteorology.

A model of soil moisture balance and herbage production for the arid and semi-arid rangelands (see Hobbs et al. 1994) was used to estimate vegetation growth and standing biomass during the study period. The model requires inputs of rainfall and potential evaporation. Calibration for the mixed open woodland landscape type in the original model is based on data from Kunoth Paddock, the paddock in which sites H1 and L1 were located (see Chapter 2), on a site “moderately to lightly grazed by livestock” (Hobbs et al. 1994) less than six kilometres from water. This distance is between those I have identified as representing high and low levels of grazing. The model does not take into consideration differences in local rainfall and grazing intensity at each site, although these factors could affect the dynamics of herbage growth. The cover of vegetation at each site was also measured directly, and differences among sites are considered in Chapters 2 and 6, but the incorporation of these data into the model was not justified considering the limited precision of the original model.

Macro-invertebrates were collected from reptile pitfall traps throughout the study (see Chapter 2). Clearly these samples only represented a small proportion of the invertebrate population and did not necessarily correspond to major prey species for lizards, but they provide a useful index of general fluctuations in the activity of invertebrates over time. Invertebrates were identified to ordinal level, counted and weighed. The total biomass of invertebrates collected during each month at each site was calculated and log-transformed to derive an index of invertebrate biomass.
Chapter 4: Temporal variation in lizard activity and abundance

Spatial and temporal organisation of data for correlations

The relationships between temperature, herbage growth and biomass and invertebrate biomass with lizard captures were considered over several different time scales; across the entire period of the study, within seasons and within defined periods of lizard activity. Data were also split according to grazing level, during the defined periods of peak activity, to determine whether any correlations between lizard abundance and climatic variables were consistent and independent of the level of grazing.

The best way to structure the data was carefully considered before analysing correlations with environmental variables. At the finest resolution in space and time, data for lizard abundance were available for each of the days trapped, at each site, although rates of capture at this resolution were extremely low and often zero. Invertebrate data were only collected for each trip, not each day within a trip, and there were no site-specific data for temperature, herbage growth or biomass. To best identify the relationship between lizard activity and environmental variables I pooled data over the three days in each trapping period and, on a spatial scale, I pooled data for sites with the same level of grazing which were sampled simultaneously. Average temperature, plant growth and biomass were calculated over each three day period of trapping. Hence, the data used for correlations consisted of two times in each month and two estimates of lizard abundance at each time (one for heavily and one for lightly grazed sites). During exploratory analyses two alternative data structures were used to ensure that the pooling of data as described did not create erroneous results: (a) each day was considered as a separate data point but all sites sampled on the same day were pooled; and (b) each site was considered as a separate data point but captures over three days were pooled. The results were very similar, regardless of the method used, except that P-values for significant correlations tended to be higher in the alternative models, because there were more replicate data points, and correlation coefficients were lower, because variation in capture rates among sites and times was introduced and corresponding data for environmental variables at these temporal and spatial scales were not available.

Results

Preliminary results

Interpretation of trapping data

Recapture rates for individual animals were too low to enable accurate estimations of abundance (Chapter 2); however, the number of captures at different sites sampled at the same time provides an index of relative abundance at these sites. Fluctuations in
captures through time reflect (a) changes in populations due to mortality, natality, immigration and emigration, (b) the percentage of the population that is active at a particular time, (c) levels of activity (e.g. time spent active and distance moved when active), and (d) the efficiency of the trapping mechanism in capturing a species at a particular time and in a particular habitat. Occasionally I use “activity” or “abundance” to describe patterns in the data where it seems logical that one or the other of these components is the main contributor to the number of captures (e.g. low captures of a non-annual species in winter is largely due to low activity rather than death or immigration). However, the extent to which each of the factors listed above contributes to the number of captures at any time is not formally defined by these data.

Abundance of lizards at sites with different grazing levels

Only one *C. nuchalis* was captured at sites with low levels of grazing but this species was trapped at all of the sites with high levels of grazing. The number of captures at heavily grazed sites varied considerably, with most captures occurring at a single site (Chapter 2). Comparisons of temporal patterns of activity at sites with different grazing levels could not be made for this species; however, temporal patterns in captures of *C. nuchalis* are considered over different time scales and compared with those of other species.

In contrast to *C. nuchalis*, when considered over the entire period of the study, both species of *Ctenotus* showed consistent trends toward higher abundance at sites with low grazing levels, a trend which is also evident for other species of skinks (Chapter 2). Captures were high enough at all sites to enable comparisons of temporal patterns at sites with different levels of grazing for these species.

No differences in the abundance of geckos were detected between sites with different grazing levels over the entire period of the study (Chapter 2). Preliminary examination of temporal patterns of activity of *D. conspicillatus*, *D. stenodactylus* and *R. ornata* showed that peaks in activity occurred in the same months for each of the three species. Sample sizes were small relative to *Ctenotus*, and so geckos were considered as a group; capture data for the three species were pooled in all analyses and also in plots of activity over time.

Comparisons of the activity and abundance of lizards across seasons and years

Results of repeated measures analysis of variance are given in Tables 4.1 and 4.2. The interaction between seasons and years was highly significant for *C. leonhardii*, *C. schomburgkii* and geckos when two years of data and four seasons were considered
Table 4.1 $P$ values from repeated measures analyses of variance of abundance ($\log(x + 1)$, where $x =$ the number of captures) of four lizard species using data from 1994 and 1995 only. The between factor is grazing level (high and low) as defined by distance from a water point and within factors are year and season and include two years and four seasons (spring, summer, autumn, winter). Results are shown for *Ctenotus leonhardii* (Cl), *Ctenotus schomburgkii* (Cs), geckos (Geck) and *Ctenophorus nuchalis* (Cn). Significant results at $P < 0.05$ are marked with an asterisk.

<table>
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<th>df</th>
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<th>Cs</th>
<th>Geck</th>
<th>Cn</th>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.0001*</td>
<td>0.0001*</td>
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Table 4.2  *P* values from repeated measures analyses of variance of abundance (log(\(x + 1\)), where \(x\) = the number of captures) using data from spring and summer only. The between factor is grazing level (high and low) as defined by distance from a water point and within factors are year and season and include three years and two seasons (spring & summer). Results are shown for *Ctenotusleonhardii* (Cl), *Ctenotus schomburgkii* (Cs), geckos (Geck) and *Ctenophorus nuchalis* (Cn). Significant results at \(P < 0.05\) are marked with an asterisk.

<table>
<thead>
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<th>Source of variation</th>
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<th>Cs</th>
<th>Geck</th>
<th>Cn</th>
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</tr>
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</table>
(Table 4.1). When three years of data but only captures in spring and summer were considered, there was a significant interaction between seasons and years for all species (Table 4.2). The null hypothesis that the relative abundance of lizards in different seasons does not differ in different years was rejected for all species. Although there were significant differences in abundance across seasons and years, there was a complex interaction between the two; no one season or year can be clearly identified with high levels of lizard activity.

A significant interaction was detected between year and grazing level for *C. schomburgkii* (Table 4.1), which suggests that abundance differed at sites with different grazing levels but that this was not consistent in different years. There was no significant difference in the abundance of *C. schomburgkii* at sites with different grazing levels over the entire period of study. The results showed that abundance of all species in seasons and years was highly variable and interactive, hence, the seasonal breakdown of data may not be the most suitable for detecting any differences between sites with different grazing levels.

**Temporal trends in activity and abundance**

**Skinks**

Distinctly peaked patterns of activity in each year were apparent for *C. leonhardii*, with no adult lizards captured during the colder months (Figure 4.2), but the months during which adult activity peaked differed in each year. In the second year of the study activity peaked in February/March and very few animals were captured in spring. This is in marked contrast with the first and third years when captures were high in October and November (spring). The asymmetry of captures in different years was even more pronounced for juvenile *C. leonhardii* (Figure 4.2). In the months when the abundance of juveniles peaked in the first two years captures consisted mainly of new hatchlings while the peak in the final year consisted of sub-adult animals (no new hatchlings had emerged). In the first year of the study, many new hatchlings were captured in January. Because no data are available from December or February, the month during which the number of hatchlings peaked is uncertain. Juvenile lizards were active during autumn but were not captured in winter. In the following spring very few sub-adult animals were captured. The apparent drop-off in activity of juveniles in December was probably an artificial result of year-old lizards attaining adult size. During the second year, in contrast, new hatchlings did not emerge until March, at least two months later than in the previous year (tracking the late peak in activity of adults). Captures were high until a sharp drop in June. Some animals
Figure 4.2 Total monthly captures of *Ctenotus leonhardii* at sites with high levels of grazing (open circles) and low levels of grazing (closed circles). Adults and juveniles are shown separately. Dashed lines indicate years as defined by the activity cycles of lizards and calendar years are also given.
remained active during winter and the number of captures increased dramatically again in spring.

Despite the dramatic variation in the timing of activity and reproduction between years, there were no obvious differences in the months during which captures peaked between sites with high and low levels of grazing, although the total number of juveniles captured at sites with low levels of grazing was consistently higher during peak periods (Figure 4.2).

Adult and juvenile *C. leonhardii* were separated in subsequent analyses because the temporal patterns of activity of each group were obviously different. Peak periods of activity for each group were identified for subsequent analyses (see Methods).

The months when captures of *C. schomburgkii* peaked (Figure 4.3) were fairly similar to those for *C. leonhardii*, although *C. schomburgkii* was active for a greater number of months. *Ctenotus schomburgkii* was the only species that was consistently trapped during the winter months, albeit in low numbers, which may reflect an ability to be active at lower temperatures or an increased likelihood of capture resulting from the generally high abundance of this species. Again, the months during which lizards were active varied markedly between years and hatchlings emerged later during the second year of the study. Periods of relatively low activity over winter were long (at least 6 months) in 1994 but only three months in 1995.

A greater number of *C. schomburgkii* were captured at sites with low levels of grazing compared to heavily grazed sites at the beginning of the period of study but this difference was not maintained in the second and third years (Figure 4.3). This result may explain the significant interaction that was detected between grazing and years for this species (Table 4.1). Monthly capture rates were more variable than for *C. leonhardii*, but despite this variability temporal trends in abundance appear to be synchronous between the two grazing levels.

Juvenile and adult *C. schomburgkii* were separated for all subsequent analyses and months when activity was high were identified, as for *C. leonhardii*.

**Geckos**

The months during which geckos were active were also different in each year (Figure 4.4), although this was not as pronounced as for skinks. The onset of activity was delayed in late 1994 compared with the other years, as for skinks, but the drop in activity in autumn was similar in 1994 and 1995. Unlike the skinks, geckos did not remain active throughout autumn and into winter in 1995; their activity was restricted
Figure 4.3 Total monthly captures of *Ctenotus schomburgkii* at sites with high levels of grazing (open circles) and low levels of grazing (closed circles). Adults and juveniles are shown separately. Dashed lines indicate years as defined by the activity cycles of lizards, and calendar years are also given.
Figure 4.4 Total monthly captures of geckos (pooled data for *Diploactylus conspicillatus*, *Diploactylus stenodactylus* and *Rhynchoedura ornata*) at sites with high levels of grazing (open circles) and low levels of grazing (closed circles). Adults and juveniles are shown separately. Dashed lines indicate years as defined by the activity cycles of lizards, and calendar years are also given.
to relatively few months during the second year. For this reason temporal trends in activity appear more regular than those for the two *Ctenotus* species.

Monthly capture rates were highly synchronous at sites with different grazing levels, and no differences in abundance between these sites was evident. The number of juvenile geckos captured was low throughout the study, and the months during which the number of captures peaked were the same as for adults. Because there was no obvious difference in temporal patterns between adults and juveniles, and because of the limited number of captures, adult and juvenile data were combined in subsequent analyses. Periods during which captures peaked in each year were identified as the focus for further analyses.

*Ctenophorus nuchalis*

Captures of the dragon, *C. nuchalis* showed a very different trend compared to the other species (Figure 4.5). A cyclic activity pattern was not evident, except perhaps for the two peaks in juvenile captures, one of which occurred in the summer of the first year and the other in autumn of the second year. An increase in abundance over the period of the study was evident. Peak periods of activity could not be identified for this species, and adults and juveniles were combined in subsequent analyses because sample sizes were too small to analyse these independently.

*Abundance of lizards at sites with different grazing levels during periods of peak activity*

There was no significant difference between the number of *C. leonhardii* captured at sites with different grazing levels in any year during months of peak activity. The mean number of adults captured at heavily grazed sites was lower in each of the three years but variability between sites was high in comparison to these differences (Figure 4.6 a). Similarly there were no significant differences in the number of newly emerged juveniles between sites with different grazing levels, although the mean number of captures at sites with low levels of grazing was higher in both years for which data were available (Figure 4.6 b).

Captures of *C. schomburgkii* and geckos at sites with different grazing levels were also compared during peak activity periods (Figures 4.7 a, 4.7 b & 4.8) and no significant differences were found in any year. Like for *C. leonhardii*, mean rates of capture of juvenile *C. schomburgkii* and geckos were higher at lightly grazed sites in all years, and rates of capture of adult *C. schomburgkii* were higher in lightly grazed sites in all but one year, but these differences were not significant.
Figure 4.5 Total monthly captures of *Ctenophorus nuchalis* at sites with high levels of grazing (captures at sites with low levels of grazing were negligible). Adults and juveniles are shown separately. Dashed lines indicate years as defined by the activity cycles of lizards, and calendar years are also given.
Figure 4.6 (a) Mean number of captures of adult \textit{Ctenotus leonhardii} at sites with high levels of grazing (open bars) and low levels of grazing (hatched bars) in the two months of peak activity in each year. (b) Mean number of captures of juvenile \textit{Ctenotus leonhardii} at sites with high levels of grazing (open bars) and low levels of grazing (hatched bars) in the first two months during which new hatchlings appeared in each of the first two years of the study. Error bars are standard errors.
Chapter 4: Temporal variation in lizard activity and abundance

Figure 4.7 (a) Mean number of captures of adult *Ctenotus schomburgkii* at sites with high levels of grazing (open bars) and low levels of grazing (hatched bars) in the two months of peak activity in each year. (b) Mean number of captures of juvenile *Ctenotus schomburgkii* at sites with high levels of grazing (open bars) and low levels of grazing (hatched bars) in the first two months during which new hatchlings appeared in each of the first two years of the study. Error bars are standard errors.
Figure 4.8 Mean number of captures of geckos (adults and juveniles pooled) at sites with high levels of grazing (open bars) and low levels of grazing (hatched bars) in the two months of peak activity in each year. Error bars are standard errors.
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Spatial variability and power of analyses

The variation in the number of captures among sites was high for all species. Because of this variability and the limited number of replicate sites the power of analyses to detect differences between sites with different grazing levels, if these existed, was limited (see also Chapter 2). Figure 4.9 shows the number of C. leonhardii captured at each site in the different seasons and years of the study. The high variation between sites at each time is clear, although there was some consistency between the relative abundance among sites at different times. For example, the consistently lower total abundance of C. leonhardii at sites with high levels of grazing (Figure 4.2 & 4.6) was mostly because abundance was low at sites H2 and H4. At the other two sites with high grazing (H1 and H3) lizard abundance was similar to that at sites with low levels of grazing (Figure 4.9).

Correlations between lizard activity and environmental variables

The rate of plant growth is an index of productivity and may be important for lizards because it affects invertebrate abundance. I anticipated that the relationship between plant growth and lizard abundance might be subject to time lags that were additional to those between rainfall and plant growth. Hence, I initially tested mean plant growth over periods of 1, 7, 14, 30, 60, 90, 120 and 180 days against the abundance of Ctenotus leonhardii, C. schomburgkii, Ctenophorus nuchalis, D. conspicillatus and R. ornata, using three different data structures (see Methods), to determine which period was most appropriate for use in further analyses at seasonal time scales and in defined activity periods. The correlation between plant growth and lizard abundance was strongest for the 4 month period (growth 4M) in 7 out of 15 cases, and for the 6 month and 1 day period in 2 out of 15 cases each. I used plant growth over the previous four months in all subsequent analyses.

Temporal variation in temperature, rainfall, modelled values for herbage growth and biomass, invertebrate biomass and lizard captures have been integrated into one figure so that the relationships between them over the entire study period can be visualised (Figure 4.10). It is clear that invertebrate biomass and lizard activity follow a similar trajectory through time (Figure 4.10 d & e) and that temperature influences this pattern. For example, monthly minimum temperatures in the first winter of the study were several degrees below average for that time of year, whereas the following winter was considerably warmer (Figure 4.10 a). This corresponds to the prolonged periods of low activity for lizards and invertebrates in the first winter of trapping compared with the second year. However, there are other factors which seem to have affected the observed abundances through time. After February 1994, there was a long period
Figure 4.9 Number of *Ctenotus leonhardii* captured at each of the eight study sites in different seasons of the study; spring (sp), summer (su) and autumn (au). Open bars are sites with high levels of grazing (H1, H2, H3, H4) and hatched bars are sites with low levels of grazing (L1, L2, L3, L4).
Chapter 4: Temporal variation in lizard activity and abundance

during which no significant rainfall occurred (Figure 4.10 b). Although temperatures rose in spring, neither lizards or invertebrates increased their activity, as they did in spring 1993 and 1995. Conditions were very dry in spring 1994 and there had been very little plant growth; consequently, standing biomass of vegetation was declining steadily (Figure 4.10 c). Lizard captures began to increase after the first rains fell in November 1994 but did not reach peak levels until after the significant rain event in January of the following year.

There are several inter-correlations among the variables considered in this section; for example between maximum and minimum temperature. Herbage growth and biomass are also correlated with temperature because estimates of vegetation growth were derived partially from temperature data. Over the 27 months of study, invertebrate biomass was also positively correlated with Tmax ($r = 0.66, P < 0.0001$), Tmin ($r = 0.74, P < 0.0001$) and plant growth ($r = 0.37, P = 0.0001$). Positive correlations between temperature and invertebrate biomass were also found in autumn (Tmax: $r = 0.72, P < 0.0001$, Tmin: $r = 0.82, P < 0.0001$) and spring (Tmin: $r = 0.47, P = 0.006$). Invertebrate biomass was also positively correlated with plant growth in autumn ($r = 0.71, P < 0.0001$) and winter ($r = 0.54, P = 0.006$). There were no significant relationships between herbage biomass and invertebrate biomass at any time.

Because the environmental variables were not independent, I did not use more than one variable in the same analysis. Instead, I tested for correlations between each variable and lizard abundance independently, over different time frames. $P$-values were adjusted according to the Bonferroni inequality because five different variables were tested against one set of data. Only correlations with $P$-values less than 0.01 were considered to be significant.

The relationship between lizard captures and environmental variables was initially tested over seasonal time periods (Table 4.3). There were significant positive correlations between temperature and lizard abundance when all seasons were considered together for C. leonhardii adults (Tmax only), C. leonhardii juveniles, C. schomburgkii adults, and geckos (see Total in Table 4.3). These correlations reflect the general trend for high captures during the warmer months and low captures during winter.

The correlations between C. leonhardii juveniles and temperature, within seasons, were generally weaker than those for adults of this species (Table 4.3 a). Ctenotus schomburgkii juveniles were significantly correlated with temperature in winter but not in any other season (Table 4.3 b), and for adults there were no significant correlations
Figure 4.10 (a) Mean monthly maximum and minimum temperatures (open squares) during the period of study and average temperatures for Alice Springs from 52 years of records (solid lines). (b) Total monthly rainfall at Hamilton Downs Station. (c) Estimates of plant growth (over the previous 4 months) and total standing biomass, modelled from climate and soil moisture data (see Methods). (d) Total biomass of invertebrates collected from pitfall traps in each month. (e) Total number of lizards captured in each month including the six species examined in detail in this chapter and 17 other species (see Chapter 2). All climate data were obtained from the Bureau of Meteorology.
Chapter 4: Temporal variation in lizard activity and abundance
Table 4.3 Correlation coefficients (r) between environmental variables and lizard captures in different seasons calculated from data collected between October 1993 and December 1995. Significant correlations are marked: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$. Sample size for each season (number of sites x number of months) is indicated in parentheses.

### a) Ctenotus leonhardii

<table>
<thead>
<tr>
<th></th>
<th>Tmin</th>
<th>Tmax</th>
<th>Growth (4 months)</th>
<th>Herbage Biomass</th>
<th>Invertebrate Biomass</th>
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</tr>
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<td>0.67***</td>
<td>0.36**</td>
<td>0.06</td>
<td>0.56***</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.73***</td>
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<tr>
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<td>0.36**</td>
<td>0.52***</td>
<td>0.22</td>
<td>0.39***</td>
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### b) Ctenotus schomburgki

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<th>Tmax</th>
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<th>Invertebrate Biomass</th>
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<td>ADULTS</td>
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### c) Geckos

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<td>0.75***</td>
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<td>0.58***</td>
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### d) Ctenophorus nuchalis

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<th>Growth (4 months)</th>
<th>Herbage Biomass</th>
<th>Invertebrate Biomass</th>
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<td>0.06</td>
<td>-0.04</td>
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<td>0.44</td>
</tr>
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<td>-0.09</td>
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</table>
Chapter 4: Temporal variation in lizard activity and abundance

between activity and temperature within seasons. Activity of *C. leonhardii* was positively correlated with maximum temperature in spring and autumn but not in summer. This was also a general trend observed for geckos and for *C. schomburgkii*, although for *C. schomburgkii* the positive relationships between activity and temperature in spring and autumn were not significant. In summer, activity was not correlated with temperature for any species and there was a negative, but not significant, relationship between temperature and the abundance of skinks and *C. nuchalis* (Table 4.3).

Differences in the relationship between temperature and activity among different seasons, and differences among species, are clear when relationships are considered over the entire period of study. Linear correlations between temperature and lizard activity for all seasons combined are given in Table 4.3, but because lizards were likely to have encountered minimum and maximum temperatures which limited activity in each year, non-linear relationships may be more appropriate for describing the response of lizards to temperature over this period. Regressions of lizard activity against temperature (Figure 4.11) highlight distinct differences among species. There was a positive correlation between lizard activity and temperature over the entire period of study for all species except *C. nuchalis* (Figure 4.11). For the two species of *Ctenotus*, activity may have been largely independent of temperature above a certain threshold (~25°C, Tmax), except when temperatures were very high and there was a slight decline in the level of activity (Figure 4.11). The relationship between gecko activity and temperature was somewhat different, as is expected for a nocturnal group. There was no evidence that activity levels of geckos declined at very high temperatures; however, activity was restricted at lower temperatures, with no geckos being caught when maximum temperatures were less than 24°C (Figure 4.11).

Because temperatures often fluctuate dramatically in spring and autumn, it is not surprising that daily temperatures were an important determinant of activity in these seasons, whereas in summer, attaining temperatures suitable for activity may be relatively easy, especially for diurnal lizards. In winter, activity was probably limited to days which were warmer than average. For geckos, the relationship between temperature and activity was more consistent among seasons (Table 4.3). The relationship between lizard activity and temperature in different seasons can largely be explained by the distribution of temperatures in each season and the relationships between the activity of each species with temperature shown in Figure 4.11.

Activity levels of *C. leonhardii* (adults and juveniles) and *C. schomburgkii* (juveniles) were correlated with plant growth over the whole period of study. Within seasons, there were also several significant positive correlations between the activity of different
Figure 4.11 The relationship between daily maximum temperature and activity of *Ctenotus leonhardii*, *Ctenotus schomburgkii*, *Ctenophorus nuchalis* and geckos. Data are the total number of lizards captured and the mean daily maximum temperature over each three day trapping period. P < 0.0001 for all regression lines shown. There was no significant relationship between the number of *Ctenophorus nuchalis* captured and daily maximum temperature.
species and plant growth (Table 4.3). The significant correlations were usually in the seasons during which each species or adult and juvenile group was most abundant (spring for adults and autumn for juveniles). The significant relationships within seasons most likely reflect differences between lizard captures across years within a season rather than short term fluctuations in activity within a season, because plant growth over the previous four months was relatively stable within each season of a particular year. Correlations between herbage biomass and the number of lizards captured also tended to be significant in the seasons when abundance was highest, although herbage biomass was also correlated with the abundance of juvenile C. schomburgkii in spring, summer and autumn.

There were few significant correlations between lizard activity and invertebrate biomass within seasons, although invertebrate biomass was positively correlated with the number of captures of each species, except C. nuchalis, when the whole year was considered.

There were few significant correlations between environmental variables and captures of C. nuchalis in any season and none over the total year.

**Comparisons during defined stages of activity**

Correlations between lizard activity and environmental variables were considered using only data for months for which activity periods were defined (early activity, peak activity and late activity for adults, emergence, post-emergence and sub-adult activity for juveniles). Data were examined to determine (a) whether correlations were consistent between sites with different grazing levels, (b) whether lizards responded differently to variables depending on the stage of activity, and (c) whether relationships differed between years depending on the timing of peak activity in each year.

The abundance of C. leonhardii adults was positively correlated with temperature during the defined activity periods (Tmax: $r = 0.54$, $P < 0.0001$, Tmin: $r = 0.47$, $P = 0.0003$) but not with any other variables. When data were split by grazing level, the correlations were only significant at sites with high levels of grazing (Tmax: $r = 0.66$, $P = 0.0001$, Tmin: $r = 0.56$, $P = 0.002$).

Separate analyses for each defined activity period revealed that the number of C. leonhardii captured was positively correlated with temperature in late activity months (Tmax: $r = 0.76$, $P = 0.0004$, Tmin: $r = 0.71$, $P = 0.001$) but not in early or peak activity months. During late activity months C. leonhardii captures were also positively correlated with plant growth ($r = 0.78$, $P = 0.0002$) and biomass ($r = 0.75$, $P = 0.0004$).
No significant correlations between captures of *C. leonhardii* and climatic variables were found when years were analysed separately, except for a positive correlation with invertebrate biomass during the activity period of the second year \((r = 0.63, P = 0.0007)\).

Captures of juvenile *C. leonhardii* were positively correlated with minimum temperatures \((r = 0.38, P = 0.004)\), plant growth \((r = 0.42, P = 0.001)\) and invertebrate biomass \((r = 0.41, P = 0.002)\) during active periods. Captures of sub-adults were not correlated with any of the tested variables, so only juveniles in emergence and post emergence months were considered further. Correlations between the activity of juveniles with temperature, plant growth and invertebrate biomass were highly significant in these months \((\text{Tmax: } r = 0.64, \text{Tmin: } r = 0.68, \text{Growth: } r = 0.68, \text{Invertebrates: } r = 0.70, P < 0.0001 \text{ for all})\). Each of these correlations was also significant when the two years were considered separately and when data for sites with different grazing levels were considered separately \((\text{all } P \text{ levels} < 0.01)\).

Captures of *C. schomburgkii* adults, in contrast to *C. leonhardii*, were not correlated with any of the tested variables during activity periods. Captures of *C. schomburgkii* juveniles were positively correlated with plant growth \((r = 0.56, P < 0.0001)\). As for *C. leonhardii* juveniles, captures of sub-adults were not correlated with any variable and only emergence and post emergence months were considered further. When sites with different grazing levels were separated, no correlations were found between juvenile activity and any other variable; however, when data were split by years, correlations between captures and temperature, plant growth, and invertebrate abundance were all significant in the second year \((\text{Tmax: } r = 0.78, P = 0.0002, \text{Tmin: } r = 0.87, P < 0.0001, \text{plant growth: } r = 0.93, P < 0.0001, \text{invertebrate biomass: } r = 0.69, P = 0.002)\) but not in the first.

Captures of geckos during activity periods were significantly correlated with temperature \((\text{Tmax: } r = 0.45, P = 0.0006, \text{Tmin: } r = 0.59, P < 0.0001)\) and this relationship was consistent at different levels of grazing. When data were split by year, minimum temperature was correlated with the activity of geckos in the second year of the study \((r = 0.78, P < 0.0001)\) but no other relationships were found. When data were split by activity period, a significant correlation between invertebrate biomass and captures in late activity months was detected \((r = 0.72, P = 0.0004)\), but no other significant relationships were found.

Relationships between activity and climatic variables are clearly different within activity periods compared to over longer time scales. The correlations between temperature and activity levels of *C. leonhardii* and geckos in each of the three activity years
Chapter 4: Temporal variation in lizard activity and abundance

(Figure 4.12) illustrate the difference in response to temperature at different time scales for different species. There was a strong positive relationship between temperature and the activity of *C. leonhardii* in the first and third years (Y1: $y = -2.07 + 0.13x - 0.001x^2$, $r^2 = 0.77$, $P < 0.0001$, Y3: $y = -0.61 + 0.05x$, $r^2 = 0.57$, $P < 0.0001$); however, in the second year, the year when activity was delayed by several months, the relationship was much weaker (Y2: $y = -2.06 + 0.18x - 0.003x^2$, $r^2 = 0.18$, $P = 0.02$). The correlation between gecko activity and temperature, in contrast, was fairly constant in all three years (Y1: $y = 0.99 + 0.05x$, $r^2 = 0.55$, $P < 0.0001$, Y2: $y = 0.68 + 0.04x$, $r^2 = 0.53$, $P < 0.0001$, Y3: $y = -0.77 + 0.04x$, $r^2 = 0.63$, $P < 0.0001$); however, the timing of activity for geckos also remained relatively constant among years compared to the other species. Annual activity cycles were more restricted by temperature for geckos than for diurnal lizards and this was consistent over short time periods. The annual activity cycle of *C. leonhardii* in different years did not consistently correspond to changes in temperature. However, activity and temperature were correlated within activity periods, particularly in the second year when activity of *C. leonhardii* was delayed.

**Discussion**

**Patterns of lizard activity and abundance over time**

The numbers of lizards captured fluctuated dramatically during the period of this study. Generally, there were annual peaks in activity in the warmer months and activity levels were low during winter months. The timing of peak activity for each species was variable in each year and, except for geckos, did not correspond closely to seasons. Annual patterns of activity also differed considerably among different taxonomic groups, suggesting that the causative factors driving changes in activity and abundance differ for different lizard families.

The patterns of lizard activity and abundance observed during this study and their relationship to environmental variables can be summarised as follows.

(a) Gecko activity was more restricted to particular seasons compared to the diurnal species, and was correlated with temperature over annual and seasonal time scales, and within active periods. For skinks, the timing of activity, annually, was flexible to a degree, but still locked into seasonal patterns and ultimately restricted by temperatures. The activity of *C. nuchalis* was very flexible and not closely tied to seasons during the study period, and was not correlated to temperature at any time scale.

(b) Temperature appeared to be an important determinant of the levels of activity of diurnal skinks in spring and autumn when temperatures are variable, and over winter, but activity was largely independent of temperature in summer.
Figure 4.12 The relationship between daily maximum temperature and the activity of *Ctenotus leonhardii* and geckos in each year of the study (Y1 = 1993/94, Y2 = 1994/95, Y3 = 1995/96). Activity of *Ctenotus leonhardii* peaked several months later in Y2 compared to the other years. Data are the total number of lizards captured and the mean daily maximum temperature over each three day trapping period. Regression equations and probabilities are given in the text.
(c) Shifts in annual activity patterns appeared to be in response to rainfall, and the effect of rainfall on productivity and invertebrate abundance.

(d) The relationship between the activity of lizards and climatic variables within the active period differed between years.

(e) Among the skinks, the activity of adults was more closely matched to fluctuations in temperature on a yearly and seasonal basis compared to juveniles. However, within active periods, juvenile activity was more closely correlated with temperature than adult activity.

Spatial and temporal patterns of activity of lizards are closely associated with the thermal environment and opportunities for activity are likely to be restricted when temperatures are very high or low. Nevertheless, through active thermoregulation, lizards are able to maintain body temperatures suitable for activity under highly variable conditions. Daily cycles of activity often vary in different seasons; for example, in winter *C. nuchalis* is only active during a brief period around mid-day but in summer activity is highest in the morning and afternoon (Heatwole 1970). Seasonal shifts in daily activity patterns, and in the use of space, enable lizards to encounter similar thermal environments during much of the year, and thereby reduce the effect of ambient temperature on daily and seasonal activity patterns. Hence, direct correlations between activity and temperature over days and seasons are likely to occur only when daily activity is substantially limited by temperature.

The consistent correlations between gecko activity and temperature suggest that activity was limited by temperature at all of the time scales considered for this group. Nocturnal species are exposed to much lower temperatures during their active period compared to diurnal species, especially in desert environments where there is often a rapid drop in temperature in the evening. However, the close alignment of patterns of activity of geckos to seasons may be due to a combination of thermal constraints and endogenous regulation of activity (Pianka & Pianka 1976; Huey et al. 1977). The reproductive capacity of geckos is constrained by having low, invariant clutch size (Ballinger 1977) and there may be selective pressures against extending the reproductive period, despite favourable weather conditions (Henle 1990). These constraints may also explain why the timing of activity was less variable between years for geckos than for other species.

Diurnal lizards, in contrast to geckos, can more easily maintain temperatures suitable for activity throughout the year by modifying their daily patterns of activity, and by using a wide range of thermal micro-habitats, which result from various degrees of shading by vegetation. The daily, seasonal and annual activity of *C. nuchalis*, for example, was not correlated with temperature during this study. *Ctenophorus nuchalis*
has a wide range of thermoregulatory behaviours; for example, burrowing and shade-seeking are both used to reduce body temperature when ambient temperatures are very high, and thermal exchange with the substrate (thigmothermy) as well as direct basking (heliothermy) are employed to increase body temperatures (Heatwole 1970). *Ctenophorus nuchalis* can also climb on to perches and so can access a greater range of thermal micro-habitats than other diurnal lizards, such as the two *Ctenotus* species, which are restricted to activity on the ground surface. In addition, *C. nuchalis* is one of the most heat-resistant species known, so physiological safety margins are wide, and lizards will accept temperatures far closer to their thermal limits than many other species (Heatwole 1970). These factors may explain why the activity of *C. nuchalis* was not correlated with daily and seasonal temperature fluctuations in this study, and why patterns of activity during the study were not aligned closely with seasons.

The abundance of *C. nuchalis* increased toward the end of the study, primarily at one site (site H4). I propose two hypotheses to explain this pattern. *Ctenophorus nuchalis* has a capacity for high rates of population growth and often invades “empty” habitats, such as are created by fire or other disturbance, but abundance drops off as other species return to an area (Bradshaw *et al.* 1991). If during 1995 conditions were less favourable for other species, and competition was reduced, *C. nuchalis* would have been able to rapidly increase in abundance, assuming that the more open habitat which characterised sites with high grazing levels (Chapter 2) was suitable for colonisation. Alternatively, if individual *C. nuchalis* are able to extend their activity, because of a wide range of thermoregulatory behaviours and a high tolerance for extreme body temperatures, they should be able to regulate activity so as to coincide with other factors such as the availability of food resources. Under this scenario the observed increase in abundance can be explained as being a result of favourable conditions, to which *C. nuchalis* was able to respond more rapidly than other species. An observed increase in body condition and growth rates of diurnal lizards in the second year of the study (Chapter 5) supports the second hypothesis, that resource availability or access to resources was higher in this year for those lizards able to maintain high levels of activity.

The timing of peak activity was also inconsistent among years for the two species of *Ctenotus*, suggesting a degree of variability in response to environmental conditions. In summer, when temperatures were high, activity levels were independent of or negatively correlated with daily temperature (Figure 4.11, Table 4.3). Reduced summer activity of diurnal lizards in arid Australia has been reported previously (Henle 1989a). The degree to which the activity of *Morethia boulengeri* is reduced in summer depends on relative amounts of shading at different sites; shade provided by tree
canopy allows prolonged summer activity but reduces winter activity (Henle 1989a). These relationships highlight the inter-dependence of habitat structure, the thermal environment, and time in providing opportunities for thermoregulation for diurnal lizards. Activity of *C. leonhardii* and *C. schomburgkii* was delayed in the second year and presumably enabled these species to make opportunistic use of increasing resources associated with rain in January and in the following months. However there may have been a trade-off; correlations with temperature during peak activity in 1995 were stronger than in other years, which suggests that daily activity within the active months was more restricted by temperatures. Presumably this was because the majority of days active were in relatively cooler seasons (autumn and winter) compared to the other years.

The activity of juvenile *Ctenotus* was also correlated with temperature within activity periods, but not when all seasons were combined. Annual activity patterns of juveniles are determined primarily by the time of hatching, which may also be directly correlated with environmental conditions. However emergence does not always occur during the warmest months of the year, which explains why activity, across all seasons, is not directly correlated with temperature. After hatching, juveniles must be active to acquire resources for rapid growth before it becomes too cold, and they commonly have higher levels of activity in winter than adults (Huey et al. 1977). Prolonged activity during winter 1995 enabled juvenile *Ctenotus* to continue to grow and accumulate fat reserves, thus compensating for late hatching in that year (Chapter 5). In comparison, adult lizards have more time to accumulate fat stores necessary for winter dormancy, after egg deposition, and so can often enter dormancy before the onset of cooler weather (Whitford & Creusere 1977). Nevertheless, my results show that adult and juvenile *Ctenotus* were active in winter 1995 and this may indicate that adults also were not able to accumulate sufficient fat stores during the spring and summer period of this year. A result of these patterns was that peak periods of activity for adults in 1995 and for juveniles in both years did not occur in the warmest months when temperature is least likely to limit activity. As a consequence, daily activity was probably more dependent on temperature during these periods. The probability of death by predation or accident can increase when lizards are active during periods when temperatures are low (Whitford & Creusere 1977), hence being active during winter is probably not an optimal strategy in evolutionary terms; however, the benefits of prolonging activity under some circumstances probably outweigh the costs in highly variable environments.

In summary, species which were less constrained by the thermal environment, either as a direct result of their physiology and behaviour or because of the range of thermal
micro-habitats to which they are exposed during their daily active period, were able to modify their annual periods of activity. Also, when annual peaks in activity did not coincide with the warmest months of the year, correlations between activity and temperature were stronger and presumably daily temperatures were more limiting to activity. In the model I proposed in the Introduction (Figure 4.1), the link between temperature and activity differs in strength for different lizard families or species which are active at different times of the day and which differ in their use of space and in their thermoregulatory behaviour.

The delay in the onset of activity in spring 1994, and the subsequent delay in the hatching of juveniles, were almost certainly responses to low rainfall in the preceding months. Rainfall is the major factor which affects productivity in desert environments and food available to arthropods (Cloudsley-Thompson & Idris 1964; Crawford 1981) and lizards (Ballinger 1977; Dunham 1978; Vitt et al. 1978). Rain can also be a direct stimulus for lizard reproductive behaviour; for example, laying of eggs may be delayed in some species until after rain (Stamps & Crews 1976; Vinegar 1975; Ballinger 1977). After the prolonged dry period which occurred during this study, summer rain may have been a direct stimulus for increasing levels of activity. However, in desert environments the long-term effects of rain on productivity are probably more important for lizards than short term weather variability. I propose that plant growth, over a period of time, may provide a suitable measurement from which to predict yearly variations in abundance or timing of activity of lizards in central Australia. Lizard activity was correlated with invertebrate abundance over the period of study, but there were few direct correlations over short time periods or within particular seasons. This was probably partly because the invertebrates collected during the study were often larger than the normal prey of lizards and some prey species were not represented. Invertebrate abundance is closely associated with plant productivity in arid environments (Cloudsley-Thompson & Idris 1964; Ayal 1994), and plant growth may actually be a better indicator of invertebrate abundance than a direct census, which will always be incomplete. Further, plant growth is easily calculated from rainfall data and incorporates differences in productivity resulting from rain in different seasons. Lag periods, such as the 4 month period used in this study, can be introduced to allow for lags between plant growth and the response of invertebrates or lizards. In other words, the relationship between plant growth and the activity of lizards (Figure 4.1) may be best measured directly, by-passing invertebrate biomass, although it is recognised that changes in the abundance of invertebrates is a likely mechanism for the relationship.
Based on the results of this study, I have revised the model presented in Figure 4.1 and have developed three alternative models to describe the activity of skinks, geckos and the agamid *C. nuchalis* (Figure 4.13). These models highlight the differences among the families in their response to different variables. For example, the activity of geckos is a strongly affected by temperature (Figure 4.13 b), but for skinks the effect of temperature on activity depends on when skinks are active and may also be influenced by the amount of plant cover (Figure 4.13 a). Temperature undeniably also affects the activity of *C. nuchalis*, but the relationship between temperature and activity is shown as a weak link (Figure 4.13 c) because at the time scales I examined no correlations between these variables were found. The relationship between plant growth and the activity of lizards which I have discussed above is represented as a direct relationship, which is not necessarily a result of links between plant growth and invertebrates and invertebrates and lizard activity. Although the abundance of prey is likely to be an important factor for lizards, lizards may not respond directly to invertebrate abundance in their patterns of activity. Instead, periods of peak activity of lizards and invertebrates may coincide because they respond to the same environmental factors. I have included plant cover and grazing as factors in the models describing the activity of skinks and *C. nuchalis*, and I will discuss this further in the following section.

The proposed relationships between annual patterns of lizard abundance, plant growth and temperature over different periods of time could be tested using independent data sets. If the relationships are verified, models such as those in Figure 4.13 could be refined so that temporal patterns in the activity of lizards could be predicted with confidence. These models would be very useful for future studies because they would enable the planning of field sampling to coincide with periods when lizard abundance was likely to be high. Periods of peak activity are probably the most important for lizards as they coincide with reproduction and juvenile emergence, but these periods do not necessarily occur in particular seasons as is often assumed.

**Comparisons between sites with different grazing levels**

Although statistical differences were not detected, mean abundance of the skink *C. leonhardii* was higher at sites with low levels of grazing in each of the three years (Figure 4.6 a & b), and mean abundance of *C. schomburgkii* was higher at these sites in the first and third years (Figure 4.7 a). For both species, the observed differences in relative abundance between sites with different grazing levels differed in magnitude through time. The variation in relative abundance at sites between different years highlights the fact that sampling populations at different times, over a range of conditions, is very important in assessing the effect of grazing on lizards in this
Figure 4.13 Conceptual models of the effect of temperature and rainfall on the activity of (a) skinks, (b) geckos, and (c) *Ctenophorus nuchalis* (see over page). These models are revised from Figure 4.1 on the basis of results from this study. Grazing and plant cover have been included as additional factors in the models for skinks and *Ctenophorus nuchalis*. Solid lines indicate strong relationships and dashed lines represent weaker relationships or relationships which were not investigated in this study. The direct relationship between plant growth and lizard activity, indicated by a grey arrow, may be useful for predicting the activity of lizards, although the functionality of the relationship is unclear. Continued over page...
Figure 4.13 ... continued. (c) Conceptual model of the effect of temperature and rainfall on the activity of *Ctenophorus nuchalis*. 
environment. In Chapter 2 I reported that skinks were more abundant at sites with low levels of grazing, but for the two skink species examined here differences in abundance were only evident at some times, and even then these apparent differences were not statistically significant. No significant differences between the abundances of the three species of geckos were detected in any year, although mean abundance was higher for sites with low levels of grazing in the final year. These results are consistent with the preliminary findings reported in Chapter 2. Geckos did not appear to be affected by differences between sites with different levels of grazing, but diurnal skinks were affected, as were agamids, which were captured almost exclusively at sites with high levels of grazing. This apparent taxonomic bias in the response of lizards to grazing is consistent with the results of an unpublished study which found that diurnal lizards were affected by sheep grazing in western New South Wales, but nocturnal lizards were not (C. James, pers. comm.).

The disparity between nocturnal and diurnal activity cycles, and the temporal patterns of activity of each species, may be crucial for understanding patterns of lizard abundance at sites with different grazing levels. The diurnal species, the skinks and C. nuchalis, which were most flexible in their response to changes in productivity throughout the study, were also the species for which differences in abundance at sites with different grazing levels were found. I suggest that the relationship between the thermal environment and the activity and abundance of each species is the link which explains these responses.

Skinks were more abundant at sites that had a high cover of ground vegetation and tree canopy (Chapter 2). I propose that the primary reason for this relationship is that skinks rely on vegetation to provide shade and shelter. I hypothesise that changes to vegetation structure, and consequently changes to the thermal environment, are the primary mechanism by which grazing affects these lizards. Because the interaction between vegetation and the thermal environment changes over time, any effects on the abundance of lizards are likely to be more evident at some times than others. Further, because diurnal lizards can modify their annual activity cycles, the ambient temperatures to which they are exposed and the importance of differences in thermal opportunities relating to structural differences in vegetation can vary substantially in different years. With additional differences between vegetation cover at different sites within each level of grazing, the relationships between the abundance of diurnally active lizards, vegetation structure and grazing become complex and highly variable over time.

In contrast, vegetation cover has much less effect on the thermal microclimates which geckos are exposed to during their active period and patterns of activity are more
closely aligned to ambient temperatures. Similarly, differences in plant cover resulting from grazing are unlikely to affect nocturnal species.

I have included grazing and plant cover as factors influencing the activity of skinks and *C. nuchalis* in Figures 4.13 (a) and (c). I consider plant cover to be a pre-existing state which may relate, for example, to habitat or grazing history. Plant growth obviously affects the absolute plant cover at a given time, but there are other components of plant cover which are independent of rainfall conditions and growth rates. In this study the standing biomass of ground vegetation as estimated from rainfall and temperature data was not correlated with lizard activity, but the estimates of standing biomass did not take into account pre-existing differences between sites (see Chapter 6). In the models (Figure 4.13) plant cover encompasses both changes in cover resulting from growth and variation in plant cover due to intrinsic differences among sites.

There were no data for temporal patterns of activity of *C. nuchalis* at sites with low levels of grazing, but for the other species, monthly fluctuations in activity were synchronous at sites with different levels of grazing. If the availability of suitable thermal micro-habitats differs at sites with different levels of grazing, as I have suggested, this did not affect the activity of lizards over long periods (of one month or more). However, the activity patterns of diurnal lizards may differ at finer temporal scales, at sites which differ in vegetation structure. There is some evidence for this; for example, in peak activity periods the activity of *C. schomburgkii* adults was more closely correlated to temperature at sites with high levels of grazing. Daily activity patterns of skinks, for which I have no data, may also differ considerably at sites with different grazing levels.

Obviously there are many other factors which determine the distribution and abundance of each species at different sites, which were not necessarily measured during this study. For example, I cannot explain why *C. nuchalis* was particularly abundant at site H2. However, the effect of vegetation cover on the thermal environment is one factor which is likely to affect all terrestrial, and diurnally active lizards. Some species, such as *C. nuchalis*, may be able to exploit these changes whereas others, such as the two species of *Ctenotus*, may be disadvantaged, at least under some conditions.

If my line of reasoning about the relationship between vegetation cover and activity in diurnal lizards is correct, then (a) differences in abundance should be more apparent at times when temperature is limiting to activity (i.e. at very high temperatures and low temperatures), and (b) differences in abundance should relate directly to the cover of vegetation at different sites, and (c), in the context of grazing, differences between
lizard abundance should be most detectable when differences in plant cover at sites with different levels of grazing are greatest. Differences between vegetation cover at different sites will be considered in Chapter 6, and the effect of these differences on the thermal environment at different times of the year and in dry and wet periods will be quantified. Nevertheless, from the data presented here it was apparent that differences between lizard abundance at sites with different levels of grazing were least evident in the second year of the study. Because activity was delayed in this year, lizards were exposed to cooler temperatures compared to the other years; hence, exposure at sites with high levels of grazing probably did not restrict the activity of lizards and may even have been an advantage on cooler days.
Chapter 5

Effect of season, climate and cattle grazing on growth and body condition of six lizard species in central Australia
Chapter 5: Growth and body condition of lizards

EFFECT OF SEASON, CLIMATE AND CATTLE GRAZING ON GROWTH AND BODY CONDITION OF SIX LIZARD SPECIES IN CENTRAL AUSTRALIA

Abstract

In the Australian arid zone, primary productivity and invertebrate abundance vary considerably over time in response to highly irregular and unpredictable precipitation. The activity and abundance of lizards is also variable, in response to these conditions and fluctuations in temperature. I measured growth rates and body condition (a measure of mass per unit body length) of six lizard species over a period of 27 months, to determine how temporal patterns of activity of each species related to changes in body condition and growth over time. Growth and body condition of lizards at sites with different levels of grazing by cattle were compared.

Among the diurnal species, *Ctenophorus nuchalis*, *Ctenotus leonhardii* and *Ctenotus schomburgkii*, growth rates and body condition varied consistently over the period of study. Body condition was low at the end of 1994 after a long dry period. In 1995, when rainfall was higher than average, activity levels were high and body condition improved. Growth rates were also higher in 1995 when lizards were active for longer, but growth rate per unit time active was comparable between the two years. The two species of *Ctenotus* had higher body condition at sites with low levels of grazing at the end of 1995 but not at other times. In contrast body condition of the geckos *Diplodactylus conspicillatus*, *Diplodactylus stenodactylus* and *Rhynchoedura ornata* did not differ between years. These nocturnal species were only active during the warmer months of the year and presumably were limited in their ability to respond opportunistically to favourable conditions in 1995.

The results suggest that rainfall, primary productivity and invertebrate abundance are important in determining the body condition and rate of growth of lizards at different times, but that temporal patterns of activity, which differ among species, are also crucial because they determine how effectively lizards can make use of available resources. Changes in the structure of vegetation as a result of grazing affect temperatures on the ground surface and so may affect activity levels, and consequently body condition and growth, of diurnal lizards at some times.
Introduction

Rates of growth and physical condition of reptiles vary greatly among species and within a species, in different geographical locations and depending on available resources at a particular time. For individual animals, variations in growth and body condition (a measure of mass per unit body length) are influenced by many factors including food availability, time available to forage, body temperature and associated effects on food-processing rate, and energy expenditure during acquisition of food or for reproduction.

Food availability and environmental temperature are the factors most commonly cited as explaining intra-specific variations in growth rates of reptiles in different places (Andrews 1976) and over time (Dunham 1978; Krekorian 1984; and see review by Bradshaw 1986). Rainfall and moisture availability can also be important indirect determinants of growth rates if rainfall affects the abundance of prey species (Krekorian 1984). In arid regions, annual variation in rainfall and the availability of food are often high and this is reflected in differences in growth rates and body condition of reptiles over time (Dunham 1978; Vitt et al. 1978; Ballinger & Congdon 1980). Moisture can also influence reptile growth directly; for example, water-deprived juvenile Anolis aeneus show limited growth even when food is abundant (Stamps & Tanaka 1981). Variation in body condition has also been attributed to changes in temperature and season (Bradshaw & De'ath 1991; James 1991a) and can also depend on reproductive activity (see James 1991a).

Body conditions and growth rates of six lizard species (two skinks, one agamid and three geckos) are examined here as part of a study on the effect of pastoralism on lizard assemblages in mulga shrublands in central Australia. The climate in this region is characterised by highly variable and unpredictable precipitation, both between years and within years, and corresponding variations in plant growth and invertebrate abundance over time (see Chapter 4). Totals for annual rainfall were 482 mm and 340 mm in the first and third years of the study, considerably higher than the average (270 mm) for this location. In contrast, the second year was a dry year with only 115 mm of rain. The monthly distribution of rain, fluctuations in temperature, and associated patterns of plant growth and invertebrate abundance during the study are described fully in Chapter 4. Annual patterns of activity and abundance of lizards varied among species and according to the environmental conditions which characterised each year (Chapter 4).

If the availability of resources is known to vary over time, we can predict that this will affect the growth and body condition of lizards. However, the time when lizards are
active will also affect the extent to which they are able to use available resources. Patterns of activity may vary in response to many factors other than changes in prey abundance, most obviously seasonal and daily fluctuations in temperature. Differences in patterns of activity among species (Chapter 4), in addition to and perhaps resulting from differences in life history, influence how effectively individuals of each species are able to access resources under different climatic conditions. Hence, both the availability of resources and the timing of activity may determine the amount of energy lizards can accumulate and subsequently transfer into growth.

Differences in grazing intensity may also affect the ability of lizards in different locations to accumulate and allocate resources for growth. Long term grazing in areas close to watering points for cattle can result in a permanent loss in productivity in the landscape or changes in the dominant plant species (Bastin et al. 1993; Pickup & Chewings 1994). Such changes potentially affect the structure of the habitat for lizards and consequently the thermal environment lizards are able to exploit, and may also affect the abundance of invertebrate prey. Through these pathways, changes in the habitat resulting from grazing may also affect the growth and body condition of lizards. No differences in total invertebrate abundance were detected between sites with different grazing levels at the study location (Chapters 2 & 4); however, only a small proportion of the invertebrate fauna was sampled. There were clear differences in the structure of both the ground vegetation and canopy cover at different levels of grazing (Chapters 2 & 6). There appeared to be differences in the effect of grazing on different lizard species (Chapter 2), and the relationship between climatic conditions, activity patterns of different species, and growth and body condition may provide the key to understanding these differences.

Growth and body condition provide a more direct measure of the current health of populations than does abundance, and measurements on individual animals may enable predictions to be made about future change in populations. Changes in growth rates and body condition also tend to occur over longer time periods, or to be more stable, compared to daily fluctuations in activity, and many of the biases associated with sampling with pitfall traps do not exist; hence, the variability of the data is reduced. Thus, measurements of these variables can provide valuable clues to the effect of environmental factors on lizard populations which are not obvious from census data alone.

Consideration of temporal patterns in growth and body condition of lizards is crucial as a background for understanding the effect of changes in the landscape on these factors and on lizard populations in general. The broad aim of this Chapter is to determine how differences in activity patterns in different years are reflected in the body condition
and growth of different species of lizards in the context of how these species respond to changes in the environment associated with grazing. Specific objectives were to (a) test whether body condition and growth of lizards differed among years, (b) test whether body condition and growth of lizards differed between sites with different grazing levels, and (c) compare trends across species.

Methods

Study sites and procedure for handling lizards

Data used to calculate body condition and growth of lizards were obtained from animals captured at eight sites on Hamilton Downs Station, approximately 60 km NW of Alice Springs in central Australia. Sites were at least 5 km distant from each other. Four sites were located within 1 km of an artificial water-point provided for stock, and represented areas with high levels of grazing. Four sites were more than 6 km from permanent water and were therefore less heavily grazed. Details of site selection and trapping design are recorded elsewhere (Chapters 2 & 4). The lizard communities at these sites were studied from October 1993 to December 1995. During this time each site was sampled with permanent pitfall traps for a period of three days in each month.

The snout-vent length (SVL) and weight of each lizard were recorded at the time of checking traps and each individual (with the exception of pygopods) was toe-clipped to enable the identification of recaptured animals. I attempted to evert hemi-penes to determine the sex of each adult lizard; however, I was not convinced that this method was reliable and so I pooled data for both sexes in all analyses. Assuming that sex ratio was constant at different times and among sites, comparisons between body condition or growth over different time periods and sites are valid despite possible variation between the sexes. Juvenile and mature lizards were distinguished based on their SVLs. Snout-vent length at maturity was defined as being 75% of maximum SVL for skinks and geckos (see Chapter 4 and Shine & Charnov 1992 for rationale) and SVL at maturity for C. nuchalis was defined as being 67 mm (Bradshaw 1981).

Calculations of body condition

For each species, body mass of each individual was plotted against SVL. Multiple measurements of body mass on recaptured individuals were not used as these were not independent and because body condition may have been affected by the trapping process. Both variables were transformed, (log_{10}x) and (log_{10}x+1) for SVL and mass respectively, to eliminate the heterogeneity of variance in the mass measure across the range of SVLs. Many lizards weighed less than one gram so adding one to mass
measurements before transformation ensured that all transformed variables were positive. The residual deviations from the fitted regressions of log SVL and log (mass + 1) for each species were used as an index of the relative condition of individual animals. Those animals falling above the line were considered to be in better condition than those animals falling below the line because they were heavier relative to their SVL. The residuals from the regressions of mass against SVL are referred to as body condition estimates hereafter.

Comparisons of body condition among years

I compared body condition of individuals over different periods which I defined according to the activity patterns of each species during the study. These periods are explicitly defined below along with a brief description of temporal patterns of activity of each species which emphasise patterns that may have affected body condition. In Chapter 4, periods of activity were defined for each species for comparison with environmental variables and to identify patterns within and between years. Some of these periods were too short to enable useful comparisons of body condition and are combined so that the focus is on comparisons of body condition among years. Hence, the periods defined here are slightly broader than those used previously in Chapter 4. Data for each year are from individuals captured across the entire activity period and so encompass any variation in body condition within that year.

For the two skinks *Ctenotus leonhardii* and *C. schomburgkii*, and the agamid *Ctenophorus nuchalis*, adults and juveniles were considered separately, because the periods when the activity of these groups peaked differed considerably (Chapter 4) and the complex array of factors influencing body condition were expected to differ between adults and juveniles. For adult lizards, each year was defined as beginning and ending in winter, but the duration of the period of activity in each year varied considerably between species. Juveniles of the two *Ctenotus* species were split into two groups for analysis, recent hatchlings and sub-adults, as these groups could be readily identified. Juveniles were considered recent hatchlings if they were captured in the period between the first evidence of emergence of hatchlings and the following winter period when activity was characteristically low. Any lizards that were active after the period of low activity in winter but which had not yet reached maturity were categorised as sub-adults. The condition of this group indicates how well juveniles survived the winter.

Once periods of activity in each year were defined, random samples of the estimates of body condition were chosen from each period so that the numbers of replicate data points in each year were equal. All analyses were performed on balanced data sets
unless otherwise stated. The condition of each group in different years was compared using analysis of variance.

_Ctenotus leonhardii_

The activity of _C. leonhardii_ during the study was characterised by distinct pulses of activity which differed in timing and duration between years (Figure 5.1). Spring activity (September - November) was low in the second year, compared to the first and third years, and newly hatched juveniles were captured later compared to the first year. The null hypothesis that there is no difference in body condition between years was tested using data from three years for _C. leonhardii_ adults over the periods defined in Figure 5.1 (a). The same null hypothesis was tested using two years data for recent hatchlings and three years data for sub-adult animals (Figure 5.1 b).

_Ctenotus schomburgkii_

Body condition of _C. schomburgkii_ was compared over the periods shown in Figure 5.2. This species was active during most months of the year and the activity periods of adults were separated by only brief periods of inactivity in winter (Figure 5.2 a). Despite being active over a greater number of months, patterns of activity for this species were similar to those for _C. leonhardii_ in that there were distinct pulses of activity in each year, particularly for juveniles. The null hypothesis that there was no difference in body condition between years was tested over three years for adults (Figure 5.2 a). Data from only two years were available for comparisons of condition of recent hatchlings (Y1, Y2) and sub-adults (Y2, Y3). Very few sub-adults were captured at the end of 1994 (Y2) so data for body condition during this period were scarce (Figure 5.2 b).

_Ctenophorus nuchalis_

_Ctenophorus nuchalis_ did not show clear cyclic patterns of activity, but there was a general increase in abundance of this species toward the end of the study (Figure 5.3 a). The lack of clear seasonal trends made it impossible to separate recent hatchlings from sub-adults. Juvenile captures were low, except in autumn of the second year, but there were enough data to compare the condition of juveniles in the first and second years (Figure 5.3 b). The body condition of adults was compared in the second and third year. Unfortunately, because captures were so low in the first year, it was not possible to compare body condition in all three years to determine whether the increase in abundance of this species during the study coincided with an increase in body condition.
Figure 5.1 Numbers of *Ctenotus leonhardii* (a) adults and (b) juveniles captured during each month the study, identifying periods coinciding with peaks in activity over which body condition was compared. For adults and juveniles the shaded areas represent the periods between which comparisons of body condition were made. Body condition of sub-adults was compared among periods indicated by cross-hatching.
Figure 5.2 Numbers of *Ctenotus schomburgkii* (a) adults and (b) juveniles captured during each month of the study identifying periods coinciding with peaks in activity over which body condition was compared. For adults and juveniles the shaded areas represent the periods between which comparisons of body condition were made. Body condition of sub-adults was compared among periods indicated by cross-hatching.
Figure 5.3 Numbers of *Ctenophorus nuchalis* (a) adults and (b) juveniles captured during each month the study identifying periods (shaded) coinciding with peaks in activity over which body condition was compared.
Geckos

The three species of gecko, Diplodactylus conspicillatus, Diplodactylus stenodactylus and Rhynchoedura ornata were captured in low numbers compared to the other species and too few juveniles were captured to enable analysis of juveniles separately. Figure 5.4 shows the periods of activity between which comparisons of body condition were made for geckos. Captures of all three species are pooled on this graph but analyses were separate for each species. The onset of activity in the second year of the study was delayed for geckos, reflecting patterns observed for Ctenotus, but there appeared to be less flexibility in temporal patterns of activity of geckos because activity dropped off in autumn in each year, regardless of when lizards first became active in that year.

Comparisons between sites with different grazing levels

The null hypothesis that there is no difference in the body condition of lizards between sites close to and distant from a water point was tested using nested analyses of variance, with sites nested in grazing levels and individuals captured at each site providing replicated measurements of body condition. For each species, this test was applied separately to data from each year. The low number of replicate measurements at some sites caused some difficulties for analyses. Unbalanced analyses of variance produce results that are unreliable and difficult to interpret (Underwood 1997). To overcome this problem a pair of replicate sites was removed from the analysis in situations where replicate measurements of body condition in one or more sites were few (<5). Data were then randomly chosen to provide equal numbers of replicates in each site. This reduced the number of degrees of freedom of the tests but made the results easier to interpret. In some cases the results of these analyses were compared with results of analyses using the complete, but unbalanced, sets of data.

Growth

Measurements of SVL of lizards that were captured more than once were used to calculate growth rate per day for individual lizards. Only recaptures which occurred on separate field trips were used because lizards captured more than once in a trip were not re-measured.

Results

Calculations of body condition

Body mass of adult lizards tended to be proportionally greater than SVL in comparison to juveniles, and the variation in mass of individuals at a given SVL was also greater in
Figure 5.4 Number of geckos captured during each month of the study, identifying periods coinciding with peaks in activity (shaded) among which body condition was compared.
mature animals. Log transformation of each variable corrected for the heterogeneous variance of body size over the range of SVLs and also linearised the relationship between mass and SVL compared to the relationship between the untransformed variables. The relationship between transformed SVL and mass for each species is shown in Figure 5.5. For two of the geckos, *Diplodactylus conspicillatus* and *Diplodactylus stenodactylus*, a linear model provided a good fit for the data. However, for both *Ctenotus* species, *Ctenophorus nuchalis* and *Rhynchoedura ornata* second order polynomial regressions described more of the variation in the data (i.e. $r^2$ values were greater). Regression equations for the relationships between SVL and mass for each species (Figure 5.5) are given in Table 5.1. Residuals from these relationships are used as an index of body condition for subsequent analyses.

It should be noted that some of the variation around the regression lines may have been due to the time each lizard had been in the trap, but any such variation would have been unbiased with respect to grazing treatment or year.

**Seasonal and yearly fluctuations in body condition**

*Ctenotus leonhardii*

No difference in the body condition of adult *C. leonhardii* was found among the three years of the study ($F_{2,147} = 0.49$, $P = 0.61$), despite peak periods of activity occurring in different months in each year and having different durations. However, body condition of sub-adult *C. leonhardii* did differ across the three years of the study ($F_{2,27} = 4.26$, $P = 0.03$). A Student-Newman-Keuls (SNK) post-hoc test showed that the mean body condition of sub-adult lizards in spring 1994 was lower than in the first and third years. The mean body condition of sub-adult *C. leonhardii* during this period, which followed a cold winter with little rain, was lower than that for juveniles (both recent hatchlings and sub-adults) at any other time. Large numbers (124/134) of estimates of body condition for sub-adults in the third year of the study were omitted from the analysis, to produce a balanced data set. As a precaution, an unbalanced analysis was also performed, using all data. The unbalanced analysis also indicated that the body condition of sub-adult *C. leonhardii* was lowest in the second year ($F_{2,158} = 9.78$, $P < 0.0001$), thereby lending strong support to the results of the balanced analysis. Juveniles that hatched in the months following the period of low body condition had significantly higher body condition compared with recent hatchlings in the first year ($F_{1,198} = 22.10$, $P < 0.0001$).
Figure 5.5 Fitted regressions between log-transformed mass and SVL for each species: *Ctenotus leonhardii*, *Ctenotus schomburgkii*, *Ctenophorus nuchalis*, *Diplodactylus conspicillatus*, *Diplodactylus stenodactylus* and *Rhynchoedura ornata*. Regression equations are shown in Table 5.1.
Table 5.1 Fitted regression models for the relationship between mass and snout-vent length \((y = \log(\text{mass} + 1), x = \log(\text{SVL}))\).

<table>
<thead>
<tr>
<th>Species</th>
<th>(N)</th>
<th>Equation</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ctenotus leonhardii</em></td>
<td>574</td>
<td>(y = 4.65 - 7.14x + 2.78x^2)</td>
<td>0.97</td>
</tr>
<tr>
<td><em>Ctenotus schomburgkii</em></td>
<td>693</td>
<td>(y = 2.46 - 4.18x + 1.79x^2)</td>
<td>0.90</td>
</tr>
<tr>
<td><em>Ctenophorus nuchalis</em></td>
<td>135</td>
<td>(y = -0.98 - 0.39x + 0.82x^2)</td>
<td>0.99</td>
</tr>
<tr>
<td><em>Diplodactylus conspicillatus</em></td>
<td>98</td>
<td>(y = -1.85 + 1.42x)</td>
<td>0.81</td>
</tr>
<tr>
<td><em>Diplodactylus stenodactylus</em></td>
<td>47</td>
<td>(y = -2.40 + 1.73x)</td>
<td>0.82</td>
</tr>
<tr>
<td><em>Rhynchoedura ornata</em></td>
<td>144</td>
<td>(y = 3.14 - 5.04x + 2.05x^2)</td>
<td>0.86</td>
</tr>
</tbody>
</table>
Chapter 5: Growth and body condition of lizards

Ctenotus schomburgkii

The body condition of adult *C. schomburgkii* differed between the three years of the study ($F_{2,31} = 4.13, P = 0.02$). A SNK multiple comparisons test indicated that body condition was significantly higher in the second and third years of the study compared with the first year. Recent hatchlings in the second year of the study were also in better condition than those that hatched in the first year ($F_{1,204} = 10.62, P = 0.001$), a result consistent with that for *C. leonhardii*. No difference was detected in the body condition of sub-adults between the second and third year of the study ($F_{1,32} = 0.02, P = 0.89$).

Ctenophorus nuchalis

There was no significant difference in the body condition of adult *C. nuchalis* between the second and third years ($F_{1,46} = 0.37, P = 0.54$). Body condition of juveniles was significantly higher in the second year of the study ($F_{2,22} = 5.84, P = 0.02$).

Geckos

No differences in body condition between years were found for *D. conspicillatus* ($F_{2,36} = 0.35, P = 0.71$), *D. stenodactylus* ($F_{2,21} = 0.78, P = 0.47$), or *R. ornata* ($F_{2,30} = 0.76, P = 0.46$).

General trends

Body condition of *Ctenotus schomburgkii* was generally higher during the second and third years of the study, despite delayed activity and hatching of juveniles in the second year. The condition of juvenile *C. nuchalis* also followed this trend. Table 5.2 lists mean values of condition for each species in each month of the study. Captures in each month were too low to permit analyses at this time scale; however, an examination of the mean values for each month is useful for further interpretation of the changes in condition identified in the analyses.

Geckos showed no discernible trend in body condition over time, which is consistent with the results of comparisons between years. For each of the other species, mean values for body condition were almost all negative during the first thirteen months of the study, suggesting that lizards were in poor condition relative to the mean condition over the whole study. Mean values for *Ctenotus schomburgkii* were almost all positive from November 1994 until the end of the study. Mean body condition of *C. leonhardii* and *C. nuchalis* remained negative until March and April 1995, respectively, after which time they reflected the positive trend found for *C. leonhardii*. Body
Table 5.2 Means of residuals from fitted regressions of mass against snout-vent length showing changes in body condition during the study period. For geckos, means were calculated from pooled data for Diplodactylus conspicillatus, Diplodactylus stenodactylus and Rhynchoedura ornata. Residuals were calculated independently for each species of gecko before pooling.

<table>
<thead>
<tr>
<th>Month</th>
<th>Ctenotus leonhardii N</th>
<th>Ctenotus schomburgkii N</th>
<th>Ctenophorus nuchalis N</th>
<th>Geckos N</th>
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<td>-0.016 46</td>
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<tr>
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<td>0.096 2</td>
<td>0.008 35</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>-0.010 8</td>
<td>-0.010 28</td>
</tr>
<tr>
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<td>-0.004 18</td>
<td>-0.033 3</td>
<td>0.000 16</td>
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<td>-0.020 3</td>
<td>0.002 4</td>
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<tr>
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<td>-0.020 30</td>
<td>-0.055 3</td>
<td>0.079 3</td>
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<tr>
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</tbody>
</table>

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condition reached a high in autumn and winter (May - August) of 1995 for all species, after which there was an apparent decline in condition in the last few months of the study. In summary, there was a shift from relatively poor condition early in the study, at its lowest toward the end of 1994 after a cool and dry winter, to relatively good condition after summer rains in 1995 and throughout the following winter. This trend was applicable to all species other than geckos. The generally poor condition of lizards in the spring of the second year occurs in conjunction with low capture rates during this period (Chapter 4 and Figures 5.1, 5.2, 5.3 & 5.4).

**Condition of Ctenotus and geckos at sites with different levels of grazing**

At several sites the numbers of *C. leonhardii* adults captured within a single year were low. For the first year, data for four sites could not be used in a balanced analysis because of low numbers captured at two of the sites with high levels of grazing. No significant difference in body condition between sites with different grazing levels was found in this year ($F_{1,36} = 0.51, P = 0.48$), but this analysis was very weak. For the second and third years, two sites were excluded from analyses, one from each level of grazing. No differences in body condition of adult *C. leonhardii* between sites with different levels of grazing were detected in these years ($Y2: F_{1,24} = 1.12, P = 0.30, Y3: F_{1,12} = 0.59, P = 0.46$). For juveniles, data were only sufficient to test recent hatchlings in the second year and sub-adults in the third year. For sub-adults only three replicate sites at each level of grazing could be used because of very low captures at the two other sites. No differences between sites with different levels of grazing were detected for juveniles ($F_{1,48} = 0.47, P = 0.50$) or sub-adults ($F_{1,66} = 0.25, P = 0.62$).

Body conditions of *C. schomburgkii* adults at sites close to and distant from water were compared in each of the three years. Data from two sites, one at each level of grazing, were excluded from these analyses because of low captures. No differences between sites with different grazing levels were detected in any of the three years ($Y1: F_{1,56} = 2.59, P = 0.11, Y2: F_{1,90} = 0.60, P = 0.44, Y3: F_{1,48} = 2.76, P = 0.10$). When all data were used in an unbalanced analysis, body condition of *C. schomburgkii* adults was lower at sites close to water with high levels of grazing in the third year of the study ($F_{1,100} = 7.575, P = 0.007$). This result should be interpreted with caution. For recent hatchlings, data from two sites were excluded from analyses. No differences in body condition at sites with different grazing levels were found for recent hatchlings in the first or second years ($Y1: F_{1,48} = 0.32, P = 0.57, Y2: F_{1,80} = 0.22$).
0.09, \( P = 0.76 \). There were insufficient data to compare the condition of sub-adults in different sites during any period.

The number of geckos captured was too low to enable any tests of differences between body condition at sites with different levels of grazing for any species at any time.

The tests described above were not strong and there were many periods when low numbers of captures at several sites made it impossible to test for differences. Mean condition indices of *C. leonhardii*, *C. schomburgkii* and geckos at sites with different levels of grazing in each year of the study are presented in Table 5.3. Adult and juvenile data were pooled for each of the *Ctenotus* species, and data for the three gecko species were pooled. For *C. leonhardii* and *C. schomburgkii* mean values of body condition at sites with high and low grazing levels were similar in the first two years (lower than the mean over the whole period in Y1 and higher in Y2), whereas in the final year, body conditions were higher than average (zero) at sites with low levels of grazing but lower than average at sites with high grazing. Formal comparisons for these species in the third year of the study were few and weak; however, the unbalanced analysis of adult data for *C. schomburgkii* also suggested that there were differences in body condition between sites with different levels of grazing in the third year. The condition of both species of *Ctenotus* may have been poorer at heavily grazed sites in the third year, although there was no evidence of any difference in the other years. Geckos had higher mean body condition at sites with low levels of grazing in all three years. The deviations from average condition (zero) were slight but this was a consistent trend.

**Seasonal and yearly growth rates**

Only three species, *Ctenotus leonhardii*, *C. schomburgkii* and *Ctenophorus nuchalis*, were captured in numbers sufficient to examine growth rates of recaptured animals. Even for these species, data were limited and the distribution of SVLs in the population over time, from which growth rates can be inferred, are presented as an additional method of comparing growth for each species.

In order to determine whether growth rates were dependent on size I calculated the SVL mid-way between the SVLs over which the growth increment was measured for each individual. The relationship between growth rates of *C. leonhardii* and mid SVL over the period of growth (Figure 5.6) was only weakly significant (\( r^2 = 0.14, \ P = 0.04 \)) and appeared to be driven largely by a few individuals which were close to their maximum size and consequently had very low growth rates. When lizards with SVLs which were close to their asymptotic maximum were removed from the analysis, there
Table 5.3 Means of residuals from fitted regressions of mass against snout-vent length (body condition) at sites with high and low levels of grazing in each year.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>High grazing</th>
<th>Low grazing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td><em>Ctenotus leonhardii</em></td>
<td>Y1</td>
<td>-0.006</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>Y2</td>
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<tr>
<td></td>
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<td>0.004</td>
</tr>
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<td><em>Ctenotus schomburgii</em></td>
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<td>Y2</td>
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<tr>
<td></td>
<td>Y3</td>
<td>-0.005</td>
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Figure 5.6 Growth rates of *Ctenotus leonhardii* relative to snout-vent length. The snout-vent lengths mid-way between those over which each growth increment was measured were used. Lizards captured at sites with low grazing levels (closed circles) and high grazing levels (open circles) are plotted separately.
was no relationship apparent ($r^2 = 0.01, P = 0.69$). This suggests that growth rate of *C. leonhardii* was independent of size for animals with SVLs of less than 65 mm. It should be noted, however, that the majority of growth records were from individuals which hatched in autumn 1995 and had not reached maturity by the end of the study. Hence, calculations of growth rates are representative of lizards with a limited range of SVLs. No difference in the range of growth rates or SVLs of lizards captured at sites with different levels of grazing were evident (Figure 5.6).

Growth trajectories of recaptured *C. leonhardii* and the SVL of each individual captured during the study are plotted against time of capture in Figure 5.7. Very few lizards were recaptured in 1994 compared with the following year (see Figure 5.7), so it was not possible to test for differences in growth rates between years. However, there was a clear correspondence between the growth of recaptured animals (Figure 5.7 a) and the shift in the distribution of SVLs (Figure 5.7 b), and growth in the population can be inferred from changes in the distribution of SVLs over time. The distribution of SVLs before and after winter in 1994 and 1995 suggests that growth rates were relatively low during months of low activity. The period of reduced activity and growth was considerably longer in 1994. Lizards hatched later in 1995 compared to the previous year; however, the number of months during which lizards were active, before winter dormancy, were approximately the same (4 months) in each year.

Sub-adult lizards captured in the spring of 1994 and 1995 were of similar size, despite juveniles hatching later in 1995. Hence, growth rates were probably higher during the second year of the study. The small number of sub-adult *C. leonhardii* captured early in the second year suggests that many lizards did not survive the winter. An alternative explanation is that all animals reached maturity before this time; however, this is not supported by the recapture records. The fact that only 3 lizards first captured in 1994 were recaptured in subsequent years also suggests that survival rates over winter 1994 were low. Nevertheless, the number of adults that did survive over winter was sufficient to produce a new cohort of juvenile lizards in the following autumn. It is not clear whether surviving adults consisted mostly of individuals which had reached maturity in the previous summer (1993/94) or recently matured lizards from the cohort hatched in early 1994.

Growth of *C. schomburgkii* was strongly dependent on SVL ($r^2 = 0.39, P < 0.0001$; Figure 5.8), with the rate of growth decreasing as lizards approached their maximum size. Determination of the sex of lizards, although not completely reliable, indicated that growth of male *C. schomburgkii* was negligible above SVLs of 42-45 mm. I was not able to evert hemi-penes for any of the individuals with greater SVLs (47-48 mm) which suggests that these lizards were probably females.
Figure 5.7 (a) Snout-vent lengths of recaptured *Ctenotus leonhardii* showing growth increments. (b) Snout-vent lengths of all *Ctenotus leonhardii* plotted against date of capture. The dashed line indicates estimated snout-vent length at maturity.
Figure 5.8 Growth rates of *Ctenotus schomburgkii* relative to snout-vent length. The snout-vent lengths mid-way between those over which each growth increment was measured were used. Lizards captured at sites with low grazing levels (closed circles) and high grazing levels (open circles) are plotted separately.
There did not appear to be any difference in the distribution of growth rates of *C. schomburgkii* between sites with different levels of grazing (Figure 5.8); however, there was considerable variation in the rate of growth of individual animals at a given SVL. When regressions were fitted to data separately for sites with different grazing levels, it was apparent that individual variation from the relationship between growth and SVL was greater at sites that were more heavily grazed (sites with low grazing: $r^2 = 0.63$, $P < 0.0001$; sites with high grazing: $r^2 = 0.26$, $P = 0.006$).

Growth trajectories for recaptured *C. schomburgkii* and the SVLs of each lizard captured were plotted against time (Figure 5.9). A considerable number of *C. schomburgkii* first captured in 1994 were subsequently recaptured (Figure 5.9 a), which may indicate that survival of this species over the cold and dry winter of 1994 was higher than for *C. leonhardii*. Alternatively, this result may reflect the higher capture rates of this species. Growth rates calculated for individuals captured and recaptured within each calendar year were used to test for differences in growth rates between years. A random sub-set of growth rates from the second year was chosen so that sample sizes were equal in each year. There was a significant difference between growth rates in the two years ($t = 2.521$, $P = 0.015$) with higher growth rates in the second year (mean = 0.037 mm/day) compared with the first year (mean = 0.022 mm/day). The same data were analysed with SVL as a covariate of growth; in this case, no difference in growth rates between years was detected (analysis of covariance: $F_{1,42} = 0.37$, $P = 0.55$). These results suggest that the uneven distribution in the size of lizards captured in each year may account for the difference in the rate of growth between years. These comparisons should be interpreted with caution because growth data for individuals of comparable size were not available in the two years. Growth rates in the first year were calculated over periods which include time after lizards had reached maturity and when growth rates had presumably begun to decline (Figure 5.9 a). In contrast, growth rates for individuals first captured in the second year of the study are calculated over a shorter period of time and were generally for individuals which had not yet reached maturity.

The distribution of SVLs of *C. schomburgkii* captured during the study (Figure 5.9 b) suggests that rates of growth of individuals of comparable size were different between years. Newly hatched *C. schomburgkii* were first captured in November 1993. No data are available for December 1993, but the number of recently hatched juveniles in January 1994 was high. By the following spring (September - November 1994), some juveniles were still present in the population, whereas many others had reached mature size (Figure 5.9 b), although it is difficult to determine from SVL distributions alone which adults belong to the cohort from the previous year. Recapture records
Figure 5.9 (a) Snout-vent lengths of recaptured *Ctenotus schomburgkii* showing growth increments. (b) Snout-vent lengths of all *Ctenotus schomburgkii* plotted against date of capture. The dashed line indicates estimated snout-vent length at maturity.
show that at least a proportion of individuals had attained adult size, probably those which hatched in spring 1993. In 1995, *C. schomburgkii* hatchlings were not recorded until February. There are no data for January 1995, but if we assume that some lizards hatched in January, then lizards hatched two months later than in the previous year. Yet although lizards hatched two months later in 1995 the SVLs of juveniles in the following spring were similar to the SVLs of juveniles captured in spring 1994. This result implies that growth rates were higher in the second year. However, because more lizards were active during the winter months of 1995 compared to the previous year (Figure 5.9 b), the number of months during which juvenile lizards were active was similar during each year. Hence the rate of growth per unit time active may have been comparable between the two years, and overall rates of growth were only lower in 1994 because growth rates were very low or zero during months when lizards were not active.

There was a significant negative relationship between growth of *Ctenophorus nuchalis* and SVL \((r^2 = 0.23, P = 0.02; \text{Figure 5.10})\) although the relationship was not as strong as for *C. schomburgkii*. Variation in growth rates, particularly among smaller lizards, was high. No growth data are available for this species during 1994 (Figure 5.11 a); however, the distribution of SVLs over time (Figure 5.11 b) provides some information on rates of growth during this period. The distribution suggests that very few adults survived between winters and that the population was mostly annual. Growth rates appear to have been higher in the second year of the study. The distribution of SVLs did not change greatly in the four months (May - August) during which lizards were inactive in 1994. In 1995 *C. nuchalis* were captured throughout winter, and the average size of the captured population continued to increase during these months.

**Discussion**

Temporal patterns of activity during the 27 months of my study varied considerably among the lizard species investigated (Chapter 4), and patterns of distribution and abundance at sites with different levels of grazing also differed among species (Chapter 2). Mean body condition of the three diurnal species *Ctenotus leonhardii, Ctenotus schomburgkii* and *Ctenophorus nuchalis* varied consistently over time. The observed patterns can be largely explained by changing climatic conditions and are discussed in detail below. Growth rates inferred from SVL distributions of captured lizards also varied consistently among years for these species, being generally lower in 1994 compared to 1995. The consistent patterns of growth and body condition among these species are strong evidence that prevailing climatic conditions and invertebrate
Figure 5.10 Growth rates of *Ctenophorus nuchalis* relative to snout-vent length. The snout-vent lengths mid-way between those over which each growth increment was measured were used. All captures were at sites with high levels of grazing.
Figure 5.11 (a) Snout-vent lengths of recaptured *Ctenophorus nuchalis* showing growth increments. All recaptures were of lizards which hatched in 1995. (b) Snout-vent lengths of all *Ctenophorus nuchalis* plotted against date of capture. The dashed line indicates estimated snout-vent length at maturity.
abundance were important determinants of growth and body condition over the period. In contrast, the three species of gecko, which are all nocturnal, did not show significant differences in body condition between years. However, according to the residuals listed in Table 5.3 there was a consistent but non-significant trend, across all years, for the body condition of geckos to be higher at sites with low levels of grazing. The two species of *Ctenotus* had higher body condition at sites with low grazing levels in the third spring and summer of the study but not in the other years. These trends would need to be investigated further before any conclusions could be drawn.

**Body condition and growth in relation to climatic conditions**

During the first few months after trapping commenced, all three diurnal species had low body condition, compared to the mean over the entire period. Condition dropped to low levels toward the end of 1994 (Table 5.2). The poor condition of lizards at this time can be attributed to the cold and dry winter, during which activity was severely limited (Chapter 4), and low levels of invertebrate activity in spring 1994 (Chapter 4: Figure 4.10). Snout-vent length distributions also indicate that growth rates were low for all three species over this period compared to the following winter. James (1991b) studied growth rates of *Ctenotus* in spinifex habitat in central Australia and found that subtracting a 90 day inactivity period from recapture intervals over winter, a period during which growth was assumed to be zero, improved the fit of Von Bertalanffy growth curves for most species. The changes in snout-vent length over winter in my study show that the period of inactivity and reduced growth in winter can vary substantially between years, and this variation should also be considered when interpreting growth rates of lizards in this environment or fitting growth models. James (1991c) found that body condition of most *Ctenotus* species were lowest during a period characterised by dry conditions and that abundance or activity was also low during the period of low body condition. These findings correspond closely with the results presented here and suggest that these patterns are consistent among a number of species and in different habitats.

Only 2 of the juvenile *C. leonhardii* first captured in 1994 were recaptured in the following summer and the distribution of SVLs of lizards captured in spring and summer 1994/1995 shows that there were few sub-adults, or recently matured adults, in the population at this time. These results indicate that mortality of juveniles was high during winter 1994 at a time when body condition was poor and growth rates were reduced. Nevertheless, the number and condition of adult *C. leonhardii* that became active after summer rains, and the subsequent reproductive output in 1995, did not appear to be affected by the sub-optimal conditions that lizards were exposed to in the previous winter and spring. For example, body condition of *C. leonhardii* was
low in spring 1994 (see Table 5.2 for other species), recruitment into the adult population was probably low, but the number of adults active in subsequent months did not differ from the previous year (Chapter 4), and juveniles which emerged in autumn had significantly higher than average condition. *Ctenotus schomburgkii* and *C. nuchalis* also had higher mean body condition in the second and third years. James (1991c) found that the abundance of adult *Ctenotus* increased markedly between two years, although there was no reproductive input into the population in the second year, and attributed this to lower levels of adult activity in the first year of his study (James 1991c). A similarly high rate of survival of adult *C. leonhardii* over winter of 1994 may explain the quick recovery of this species both in terms of body condition and reproductive output after summer rains in early 1995.

Low temperatures in spring can limit activity time and subsequent clutch frequency of lizards in Nebraska (Jones *et al.* 1987). In central Australia, spring activity was low in 1994, when rainfall was very low, however this did not appear to affect reproductive output in the following autumn. A period of low rainfall, low abundance of lizards and poor body condition is also reported by James (1991c). Although this period was in autumn, in contrast to the dry spring which occurred during my work, subsequent reproduction was not affected in either study. Warm temperatures at my sites in winter 1995 enabled juvenile *C. leonhardii* and *C. schomburgkii* to maintain high levels of activity and probably compensated for delayed reproduction and later hatching in this year. Although reproduction and activity of *Ctenotus* are locked into seasonal time-frames to varying degrees for different species, rapid response to rainfall occurring in different seasons is obviously possible. This is undoubtedly important in an environment where rainfall is erratic and not associated with a particular season.

Flexibility in activity and reproduction of lizards in response to rainfall is common in arid environments and probably reflects an evolutionarily successful strategy for maximising reproductive success (Vitt *et al.* 1978). There is no evidence that low rainfall in 1994 resulted in any permanent changes in lizard abundance in the subsequent year, despite low recruitment and delayed reproduction. However, the variation in rainfall during my study was not unusual for this location. Records for Hamilton Downs Station since 1958 show that periods when rainfall was below average in three or more consecutive years have occurred on four occasions, including the three years prior to the current study, 1990 - 1992. The effect of such prolonged periods of drought potentially have more dramatic effects on lizard populations.

Mean condition of *Ctenophorus nuchalis*, like for the *Ctenotus* species, was higher toward the end of the study. But this species differs from the others considered here in that it occurred almost exclusively at sites with high levels of grazing and because there
Chapter 5: Growth and body condition of lizards

were no clear peaks in captures in the warmer months of the year. Ctenophorus nuchalis has been described as an invading species which specialises in populating habitats in which lizards are scarce, and it has the capacity for high rates of increase under favourable conditions (Bradshaw et al. 1991). In Chapter 4, two hypotheses were proposed to explain the increase in abundance of C. nuchalis during this study. The first was that C. nuchalis can rapidly increase in abundance when conditions are unfavourable for other species, and hence competition is decreased. The second was that C. nuchalis is able to increase in abundance more rapidly compared to other species when resources are plentiful by maintaining high levels of activity under a range of conditions. The general increase in body condition of each of the diurnal lizards indicates that resources became more accessible, or the ability to assimilate resources improved, toward the end of the study. This supports the second hypothesis; that C. nuchalis is able to increase in abundance more rapidly compared to other species, under favourable conditions.

Correlations between rainfall and growth rates of lizards in arid regions have been well documented and are commonly attributed to food availability (Vinegar 1975; Krekorian 1984). Dunham (1978) provided convincing evidence that invertebrate abundance is serially correlated with rainfall, that individual foraging success of Sceloporus merriami is correlated with estimated prey abundance and that variation in food availability results in predictable variation in growth rates. Direct correlations between abundance of prey and increase in fat reserves have also been reported (Licht 1974). However, changes in invertebrate abundance alone cannot explain the trends in changing body condition and growth of diurnal lizards in this study and their relationship to climatic conditions as described above.

The positive correlation between lizard activity and invertebrate abundance during the period when my study was undertaken has been described elsewhere (Chapter 4). It is not clear whether this correlation represents a functional relationship or whether lizards and invertebrates respond to the same environmental conditions, particularly since data for invertebrate abundance did not correspond to primary prey species. Some relationships between invertebrate abundance and growth and body condition of lizards over the period of this study are evident. Invertebrate abundance was low when body conditions of lizards declined, during the winter and spring of 1994 (Chapter 4). Invertebrate populations did not increase until January and February 1995, corresponding with an increase in lizard activity and higher body conditions of active lizards, both adults and recent hatchlings. However, lizards remained active in high numbers during autumn (March - May) 1995 and reached peak levels of condition during this time, whereas invertebrate abundance had begun to decrease substantially.
In March (see Chapter 4, Figure 4.10). Invertebrate abundance increased again in September along with the number of active lizards; however, the body condition of lizards did not improve. A gradual decline in condition was apparent at this time for all species (Table 5.2). The progressively lower abundance of invertebrates in the second and third years did not correspond to the trend for increasing body condition of lizards over the three years of the study.

Two other studies of lizards in central Australia found that the relationship between growth of lizards and invertebrate abundance was not straightforward. James (1991b) found no difference in growth rates of most species of *Ctenotus* in two years although variation in rainfall and food abundance between years was high. Henle (1989a) compared growth rates of *Morethia boulengeri* in two years and found that these lizards grew more rapidly in the year during which prey availability was lower. He proposed that because population density was also lower in this year, the ratio of resource availability to demand was higher in the year with higher growth rates (Henle 1989a). It is apparent from the current study that time spent active, which presumably determines the potential for acquisition of available resources, is as important as the absolute abundance of food for lizards in this environment.

Another result which is not immediately explicable in terms of changing invertebrate abundance is the generally low body condition of lizards captured during the first few months of the study. Rainfall was high over this period and plant productivity and invertebrate abundance was also high relative to any other time during the study (Chapter 4). A possible explanation may be that unusually high temperatures in the summer of 1993/1994, particularly during days of trapping, may have restricted the activity of lizards and hence the time that could be spent foraging and acquiring fat reserves, although capture rates were high during this time. Lizards captured during this period may have also suffered greater levels of dehydration, while confined in traps, relative to lizards captured during other times of the study. If these animals were water-stressed, low mass to length ratios could be falsely interpreted as representing lower body condition when in fact they actually represent partial dehydration. It is important to consider that body condition, as measured in this study, does not necessarily relate directly to fat reserves and can be affected by many other factors.

Geckos, unlike *Ctenotus* and *C. nuchalis*, did not show any differences in body condition between years. The temporal patterns of activity of geckos observed during the study (Chapter 4 and see methods), suggest that opportunities for geckos to extend their active period into autumn and winter are limited, perhaps because of endogenous rhythms or because of thermal constraints relating to nocturnal temperatures (see Chapter 4). Because gecko activity is restricted to the warmest months of the year,
differences in the availability of resources between years may be critical. We might predict that low spring activity in the second year of this study would be reflected in poor body condition and slower growth rates during this year. This was not the case. No data are available for the growth rates of geckos during the study, but mean body condition in the second year was not significantly different from the other years (Table 5.3).

*Diplodactylus conspicillatus* and *Rhynchoedura ornata* are both termite specialists (Pianka 1986). Termites may be widely available as prey during periods of otherwise low productivity (Morton & James 1988) and many species of *Ctenotus* consume mostly termites when the abundance of other prey is low (James 1991d). If termites were available in sufficient numbers in spring and summer of 1994 this may explain why body condition of geckos remained relatively stable compared to the other species; it does not explain why the two species of *Ctenotus* had low body condition at this time, assuming they are also able to access this resource.

An alternative explanation for why geckos maintained their body condition in the second year, when the other species did not, relates to differences in patterns of activity among nocturnal and diurnal species. The activity of diurnal lizards may have been limited in spring 1994 because standing biomass of vegetation was low (Chapter 4) and shelter opportunities at ground level were fewer than at other times. Opportunities for diurnal lizards to forage would have been fewer over this time, as well as the abundance of prey being lower. Geckos would not have been affected by the lack of shelter, so provided that some prey species were active, even if in low numbers, geckos may have been able to access sufficient resources to maintain high levels of body condition. On the other hand, because the annual activity of geckos was more restricted by seasonal changes in temperature (Chapter 4), they were not able to extend their activity period into autumn and winter 1995 like the diurnal lizards. I believe that this line of reasoning provides a highly plausible explanation of why the body condition of geckos did not increase during this year.

**Body condition in relation to grazing**

Body condition of geckos tended to be lower at sites close to a water point, with high grazing levels, although this trend was not significant. It is unlikely that termite populations have decreased at sites with high levels of grazing; sheep grazing did not affect termite populations in wandoo (*Eucalyptus capillosa*) woodland in the Western Australian wheat-belt (Abensperg-Traun 1992), and in other studies grazing by large herbivores has been found to result in greater abundance of termites (Watson & Gay 1970; Braithwaite *et al.* 1984). Geckos at sites with high levels of grazing may be
more restricted in the time they can spend active, perhaps because of increased rates of
heat loss from the ground due to lower vegetation cover. However, if limits to the
time available to acquire resources are responsible for observed variation in body
condition, then it should have been lower among geckos in the second year of the
study when the number of active months was fewer. If geckos really are
disadvantaged at sites with high grazing levels, why is this not reflected in the size of
populations? More data for geckos are required before inferences on changes in body
condition between sites with different grazing levels can be made with any confidence.

There was a significant difference in the body condition of *C. schomburgkii* adults at
sites with different grazing levels in the third year of the study, and mean condition
was higher at sites with low levels of grazing across all size classes for *C.
schomburgkii* and *C. leonhardii* during this year. The study by Griffiths and Christian
(1996) is the only other work which has compared the body condition of lizards at
sites subject to different management practices over a range of time periods. Frill­
necked lizards (*Chlamydosaurus kingii*) in northern Australia, at sites which have been
burnt, have higher body condition in the wet season compared to lizards in unburnt
areas (Griffiths & Christian 1996). This result was related to the amount of prey
taken; both the abundance and accessibility of prey are considerably enhanced by
burning (Griffiths & Christian 1996). In contrast, no differences in the abundance of
invertebrates between sites with different grazing levels were detected during my study
(Chapter 3). Nevertheless, structural differences between sites with high and low
grazing levels may have been greater in the third year compared to other times (Chapter
6). The activity of skinks may have been limited by the thermal environment, or more
time may have been spent in thermoregulatory behaviours, at the more exposed sites
with high levels of grazing, in 1995. As a result, lizards may not have been able to
forage as effectively, or have had the same access to resources as in sites with higher
ground cover.

**Conclusions**

In summary, the results show that there is a close relationship between the level of
activity at a particular time and rates of growth and body condition of lizards in the
mulga shrubland environment. Although periods of high activity may correspond with
increased abundance of prey, the time spent active, and the ability to access food
resources, is probably more important than invertebrate abundance itself in determining
growth and body condition of lizards. For example, geckos were not able to maintain
high levels of activity in autumn and winter of 1995 and did not show a general
increase in body condition over this period. Exposure to higher and more diverse
temperatures during the day, combined with precise thermoregulation, enables diurnal
lizards to modify their annual patterns of activity (Chapter 4) and to respond opportunistically to favourable conditions. Hence, body condition and growth patterns for these species vary more directly and predictably with changes in primary productivity over time.

In Chapter 4, I suggested that grazing may affect diurnal lizards because changes in the structure of vegetation affect the thermal micro-habitats which these lizards can exploit during their daily active periods. Similarly, differences in vegetation cover over time, in response to the level of rainfall, may limit activity under certain conditions. In contrast the effect of vegetation on the thermal environment is probably irrelevant for nocturnally active, ground dwelling lizards. Although diurnal lizards can more easily respond to favourable conditions during periods of high rainfall than nocturnal lizards, the interaction between vegetation structure and the thermal environment may limit opportunities for diurnal lizards to be active at some times, and hence may also limit their ability to acquire resources for growth and accumulation of fat reserves. Relationships between vegetation structure, the thermal environment and lizard activity are explored in the next chapter.
Chapter 6

Changes in vegetation cover and lizard abundance at sites with different levels of grazing in a dry and wet year in mulga shrubland habitat, central Australia
Chapter 6: Relationships between vegetation cover, grazing and lizard abundance

CHANGES IN VEGETATION COVER AND LIZARD ABUNDANCE AT SITES WITH DIFFERENT LEVELS OF GRAZING IN A DRY AND WET YEAR IN MULGA SHRUBLAND HABITAT, CENTRAL AUSTRALIA

Abstract

Grazing is generally associated with a reduction in vegetation cover which may in turn affect the abundance of some lizard species. However, in environments characterised by extreme temporal variation in rainfall, vegetation cover can change dramatically over short periods and the impact of grazing can vary considerably in space and time. Structural characteristics of vegetation at eight sites with different levels of grazing were compared with the relative abundance of lizards captured at each site in spring of a dry and a wet year. The relative cover of ground vegetation among sites was not consistent between years, but despite this variation, the abundance of skinks was positively correlated with the cover of ground vegetation at different sites in both years. In the dry year, when abundance of lizards was low, there was no significant difference in the number of skinks captured, or the cover of ground vegetation, between sites with high and low levels of grazing. In the wet year the cover of vegetation was higher at sites with low levels of grazing and the abundance of skinks was also higher at these sites. Canopy cover was also higher at sites with low levels of grazing and shaded micro-habitats were more common across space and time at these sites. Shrub canopy and ground vegetation may both provide important sources of cover for diurnally active lizards when temperatures are very high. Skinks are species that forage widely and so they are exposed to a range of thermal micro-habitats which vary according to vegetation cover. Also, most foraging activity probably takes place within and around clumps of grass. The effect of grazing on skink abundance appears to be related to differences in ground vegetation among sites in this environment and is not always perceptible because the cover of vegetation is highly variable over space and time.

The abundance of geckos, pygopods and agamids did not correlate with the cover of ground vegetation or canopy cover in either of the two years. Geckos and pygopods may not be affected by grazing because vegetation cover has less effect on the thermal environment during the time when nocturnal species are active. Agamids, like skinks, are heliothermic, diurnally active lizards, but their physiology, foraging mode and thermoregulatory behaviour differ considerably from skinks. These species are less likely to be adversely affected by high temperatures and probably benefit from large areas of open ground if suitable perches are also available from which to forage.
Introduction

The structure of vegetation is an important determinant of the distribution and abundance of lizards. Complex vegetation structures provide a diversity of habitats and opportunities for many species, and positive relationships between the structural complexity of the vegetation and the diversity of lizards have been demonstrated in many studies (e.g. Pianka 1966; Kitchener et al. 1980; Hadden & Westbrooke 1996). Of the few studies in North American deserts which have investigated the effect of grazing on lizard diversity and abundance, all have attributed changes in species richness and composition to changes in the structure of the habitat (Busack & Bury 1974; Jones 1981; Bock et al. 1990) although vegetation cover was not measured quantitatively in these studies. Jones (1981) found that grazing only affected lizard abundance and diversity in vegetation communities that were affected structurally by grazing.

In arid Australia grazing activity is usually concentrated around artificial water points provided for stock. A gradient of gradually increasing cover of ground vegetation with increasing distance from water often results (Pickup 1989) although, if there is an increase in plant species which are unpalatable to grazing animals close to water, an inverse gradient or composite gradient may occur (Bastin et al. 1993). Inverse gradients may be temporary when they are associated with a flush of ephemeral species close to water. Grazing gradients can vary considerably at different times. For example there may be substantial recovery of vegetation in areas which are heavily grazed after rain and the gradient may disappear or become less noticeable. Short term variability in rainfall can result in dramatic changes in vegetation cover. In addition, the response of vegetation to rainfall and the impact of grazing on plant cover are highly variable across space. These factors make it difficult to assess permanent degradation in vegetation communities in rangelands (Pickup et al. 1998), let alone in animal communities which might be responding to these changes. If lizard communities are affected by grazing because of changes in the structural environment, as has been implicated in previous studies (e.g. Jones 1981), then it is not surprising that differences between lizard communities at sites with different grazing levels are not consistent at different times in highly variable environments such as the central Australian desert (Chapters 4 & 5). But how quickly do the abundances of species which are associated with structural components of the vegetation change? Does the abundance of lizards only change in areas where productive potential has been permanently lost or do lizards respond to short term changes in vegetation structure?
Chapter 6: Relationships between vegetation cover, grazing and lizard abundance

In the mulga environment, grazing gradients, relating to vegetation cover, usually do not extend far from water points compared to some other habitats; nevertheless, a reduction in ground cover is usually evident close to water points. Canopy cover may also be lower in areas which are heavily grazed. This may be partly due to the practice of cutting mulga to use as forage in dry periods, although this is not common in central Australia, or as a result of direct damage to trees and shrubs by cattle. The rate of regeneration of woody trees and shrubs can be very low in these areas because recruitment only occurs under exceptional climatic sequences and grazing prevents recruitment at these times (Crisp 1978; Cheal 1993).

Most of the lizards examined in this study are active on the ground, and there are several ways in which vegetation structure may be important for these species: (a) the cover of vegetation directly affects the thermal environment to which lizards are exposed, or are able to exploit, at different times of the day and in different seasons; (b) the distribution of invertebrate prey may be associated with particular vegetation types; (c) vegetation may provide shelter from predators.

The thermal environment imposes constraints on the activity of lizards depending on the spatial availability of acceptable thermal microclimates at a given time within the home range (Christian et al. 1983; Grant & Dunham 1988). This relationship may be particularly important at times when environmental temperatures are extreme. In central Australia, activity may be constrained in mid-summer because a large proportion of the home range is too hot to enable activity during most of the day. In contrast, mid-winter temperatures may be too low to enable a lizard to attain body temperatures optimal for activity. The thermal micro-habitats to which lizards are exposed can be influenced by ground cover and the availability of shade from trees as well as ambient temperatures, wind speed and reflectance of the substrate (Christian & Tracy 1981). Nevertheless, changes in the availability of thermal micro-habitats which result from differences in vegetation structures are likely to be important only for species which are active during the day. Morton et al. (1996) predicted that alterations to the composition of reptile assemblages in Australian rangelands, in response to grazing, may be more apparent for diurnal species, because they are more likely to be affected by structural differences in vegetation.

Alternatively, if the primary importance of vegetation structure for lizards is related to their mode of foraging, then a distinction between nocturnal and diurnal species may not be obvious. Jones (1981) found that widely foraging lizard species are most affected by grazing, having lower abundance at sites with heavy grazing, whereas some sit-and-wait foragers are more abundant in areas with high levels of grazing. It
may be possible to predict the response of lizards to grazing according to a combination of their primary foraging strategy and their time of activity.

The results presented throughout this thesis show that in central Australia, in the mulga environment, skinks tended to be more abundant at sites with low levels of grazing compared to heavily grazed sites, but this pattern was not consistent through time (Chapter 4), and there was considerable variation in the abundance of skinks among sites (Chapter 2). In contrast I have found no clear evidence that the abundance of geckos differed at sites with different levels of grazing. *Ctenophorus nuchalis*, the only species which was significantly more abundant at sites with high levels of grazing (Chapter 2), is a diurnally active, sit-and-wait predator which is highly successful in open areas (Heatwole 1970; Pianka 1971b). I have proposed that, for diurnal lizards, the interaction between vegetation structure and thermal microenvironments might be the most important difference between sites with different grazing levels. I have demonstrated that the abundance of lizards, particularly skinks, is correlated with plant growth and standing biomass in some seasons (Chapter 4); however, these correlations were based on estimated herbage biomass and did not incorporate differences between sites. In this chapter I will compare the abundance of lizards at each of the study sites directly with structural components of the vegetation in two years and will consider both spatial and temporal variation in the cover of vegetation.

The objectives of this study were to:

(a) compare the cover of ground vegetation at the eight study sites in a dry period and a wet period;
(b) compare canopy cover at the eight study sites and determine the amount of cover, in terms of sun and shade, which the canopy would produce for ground-active lizards at different times of the day and year;
(c) compare the relative abundance of ground dwelling lizards at sites with different grazing levels in the dry and wet period; and,
(d) test whether the abundance of skinks is correlated with vegetation cover at different times.

**Methods**

**Description of study sites**

I conducted the study on Hamilton Downs Station, a pastoral holding north-west of Alice Springs in central Australia. Study sites were all located in groved, tall mulga shrubland habitat (Lendon & Ross 1978) which is dominated by an over-storey of *Acacia aneura*. Perennial grasses, such as woollybutt grass (*Eragrostis eriopoda*), are
dominant in run-on areas, under and at the edge of mulga groves, and ephemeral species, such as *Aristida contorta*, are common in intergrove (run-off) areas (Lendon & Ross 1978). Four study sites (H1, H2, H3, H4) were located within 1 km of an artificial water point for cattle and were categorised as having high levels of grazing. An additional four sites (L1, L2, L3, L4) were located more than 6 km from the nearest water point and were categorised as having low levels of grazing (see Chapter 2 for maps showing site location).

**Measurement of ground vegetation**

I measured ground vegetation at each site in September 1994 and again in June 1995. I chose the period in September 1994 to represent a dry period during which growth and standing biomass of vegetation were low. Average annual rainfall in the region is 270 mm but total rainfall in 1994 was only 115 mm and very little rain had fallen in the six months prior to measuring vegetation in September (Figure 6.1). Standing biomass of vegetation (i.e. grass, herbs and forbs), modelled from rainfall data (see Chapter 4), is also shown in Figure 6.1. The second period, June 1995, followed a period of high rainfall. According to the model, standing biomass of vegetation was higher than in the first year and was increasing (Figure 6.1). Total annual rainfall in 1995 was 340 mm.

At each study site, 40 permanent pitfall traps, arranged in pairs, were installed to capture lizards. Traps in each pair were connected by 10 m of drift fencing. Paired traps were situated on a 30 x 30 m grid, of 4 x 5 trap pairs, so the total area covered by traps was 120 x 150 m (see Chapter 2). At each trap unit, I estimated the cover of vegetation in ten quadrats of 1 m x 1 m. I placed five quadrats along each side of the drift fence associated with each trap, evenly spaced, approximately 1.5 m apart (Figure 6.2). Quadrats were placed two metres out from the drift fence to avoid the area immediately adjacent to each drift fence which had been disturbed by frequent checking of traps. I estimated the percentage cover of standing vegetation (grass, herbs, forbs) in each of the 200 quadrats at each site. Because the traps were originally placed on a grid and their position relative to the vegetation was random, the quadrats provided a non-biased representation of the vegetation in each site.

**Measurement of shade**

The proportion of shade at ground level, produced by the tree canopy, was estimated at each site. A 10 m length of measuring tape was placed along the side of each drift fence used for capturing lizards (Figure 6.2) and the proportion of shade and sun on each transect was recorded. I measured shade at each site at approximately 1230 h in December when the sun is almost directly overhead, at 1530 h in December, and at 139
Figure 6.1 Monthly rainfall (bars) and estimated herbage biomass (solid line) in 1994 and 1995 at Hamilton Downs Station. Biomass was modelled from rainfall data (see Chapter 3) and neither the rainfall data or the predicted values for herbage biomass incorporate differences between sites. The approximate time when ground vegetation was measured at each site is shown by the dashed lines. Data for lizards captured in spring in both years (months are underlined) were used to compare lizard abundance and ground vegetation at each site.
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Figure 6.2 The lay-out of pitfall traps and drift-fences used for capturing lizards at each of the eight study sites. The area surrounding one trap is shown in detail. Squares indicate the approximate position of quadrats used to estimate the cover of ground vegetation and the dashed line indicates the position of the transects along which the percent of shade on the ground was measured relative to pitfall traps.
1530 h in June when sun angle was low. Measurements for each site were made on different days and took approximately one hour. Because sun angle is a function of time of day, date and latitude, there were slight differences in the angle of the sun when shade was measured at each site. I determined the exact sun angle at the midpoint of time during which shade was measured at each site using Voyager® software. From these data I determined the relationship between sun angle and the amount of sunlight, or shade, on the ground and made predictions about the proportion of sun and shade at each site at other sun angles, at different times of the year or day.

**Temperature data**

Temperatures on the ground were measured at hourly intervals, on a clear day in spring, to determine the approximate range of temperatures available to lizards in a day. Each hour 40 spot temperatures (approximately 12 cm in diameter) were taken in both shade and sun microhabitats, and mean temperatures in the sun and shade were calculated. Temperatures were measured, to the nearest degree, with a Raytex® non-contact thermometer.

**Lizard abundance and activity**

Details of the design of traps for catching lizards, materials used and the location of sites are given fully in Chapter 2. Pitfall traps were opened for four days in each month during a period of 27 months (see Chapter 4), but I only examine data for spring 1994 and spring 1995 in detail in this chapter. These periods correspond with the high and low rainfall periods when I measured ground vegetation. I only used data from spring to avoid the effect of seasonal differences in temperature on lizard activity and abundance. Although vegetation was measured in June in 1995, several months before spring, it is reasonable to assume that changes in vegetation cover were small over this time period, and this is supported by modelled estimates of herbage biomass over the period (Figure 6.1). Data for the abundance of lizards in summer 1994/95 and autumn 1995 are also presented for some species although there are no corresponding data for ground vegetation at these times.

Lizards were considered in broad groups of species which corresponded to taxonomic families. The criteria used to group species are described in the Results. Data for individual species are also examined in some cases; however, the number of captures of each species at each site in spring was low, especially in 1994, so random noise in the data may account for a considerable part of the observed variation in captures at each site.
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Results

Variation in the cover of vegetation and the degree of shading over time

The cover of ground vegetation differed considerably among sites and between September 1994 and June 1995 (Figure 6.3). Vegetation cover was higher in 1995 compared to the drier period in 1994 in all sites except L2. Generally, cover was higher at sites far from a water point except at L3 where vegetation at ground level was sparse in 1994 but increased considerably after the wetter period in 1995. Sites which had the lowest cover in the dry period (1994) generally showed the greatest response to rain. There was substantial response in terms of vegetation cover at sites with high levels of grazing and at site L3 which had low levels of grazing, but also had low cover in 1994.

Unlike grasses and herbs at ground level, canopy cover does not change rapidly in response to rainfall, although production of leaf material and leaf orientation may vary. I assumed that canopy cover did not change during the study period and estimates of the amount of shade produced by the tree canopy were only under taken in 1994, at times when the sun angle differed as described in the methods. The percentages of the ground in sunlight measured at three different sun angles, at the eight sites, are plotted in Figure 6.4. Because the area of the ground in the sun, at a given sun angle, was universally greater at sites with high levels of grazing, only two regression lines were fitted to the data initially, to represent the generic relationship between sun angle and sun-light on the ground for each level of grazing, based on measurements at all sites within each grazing level (Figure 6.4). Regression lines were also fitted for each site individually to enable more detailed comparisons of the proportion of sun and shade among sites (equations are given in Table 6.1).

In the morning and the afternoon, when the acute angle of the sun to the ground is the same, the percent of the ground in sunlight should also be the same, on average, at a given site. I assumed that this was true at the study sites and duplicated data to obtain values for the percent of sun and shade for sun angles between 90 and 180 degrees and to force the regressions to be symmetrical about the 90 degree point.

The fitted regressions for sites with high levels of grazing \( y = 4.70 + 1.38x - 0.008x^2 \) and low levels of grazing \( y = -15.87 + 1.49x - 0.008x^2 \), where \( x \) = the sun angle, were used to calculate the percent of the ground expected to be in full sunlight at different times of the day and year. The proportion of the ground in sunlight was much higher at sites with high grazing levels (Figure 6.5). For example, the proportion of the ground in sunlight, at equinox, at sites with low levels of grazing
Figure 6.3 Mean cover of vegetation at each site after a dry period in September 1994 (squares) and a wet period in June 1995 (triangles) at each of the study sites.
Figure 6.4  Percent of the ground in full sun-light in relation to sun angle. Data are for four sites with high levels of grazing (open circles) and four sites with low levels of grazing (closed circles). Each regression line is fitted to data from all sites within a grazing level. Regression equations are given in the text.
Table 6.1  Fitted regression models used to predict ground in full sun-light \((y)\) according to sun angle \((x)\) at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Regression equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td>(y = 11.14 + 1.31x - 0.007x^2)</td>
</tr>
<tr>
<td>H2</td>
<td>(y = 4.18 + 1.34x - 0.007x^2)</td>
</tr>
<tr>
<td>H3</td>
<td>(y = 7.39 + 1.35x - 0.008x^2)</td>
</tr>
<tr>
<td>H4</td>
<td>(y = -3.17 + 1.49x - 0.008x^2)</td>
</tr>
<tr>
<td>L1</td>
<td>(y = -17.95 + 1.69x - 0.009x^2)</td>
</tr>
<tr>
<td>L2</td>
<td>(y = -5.16 + 0.96x - 0.005x^2)</td>
</tr>
<tr>
<td>L3</td>
<td>(y = -15.47 + 1.54x - 0.008x^2)</td>
</tr>
<tr>
<td>L4</td>
<td>(y = -24.01 + 1.74x - 0.01x^2)</td>
</tr>
</tbody>
</table>
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Figure 6.5 The area of the ground in full sun-light during a clear day in mid-summer, at equinox, and in mid-winter at sites with high and low levels of grazing. Graphs represent mean estimates of the area of sun and shade for sites at each grazing level and are derived from the fitted regressions shown in Figure 6.4.
was similar, throughout the day, to the amount of sun on the ground in mid-winter at sites with high levels of grazing.

Temperatures in the sun and in the shade differ greatly depending on the time of day and year, and hence the differences in the availability of sun and shade may be significant for lizards at some times but not at others. Profiles of ground temperatures in shaded and sun-lit microhabitats for a typical spring day (maximum temperature = 37°C) are shown in Figure 6.6. The temperature above which lizards become incapable of escaping conditions which ultimately lead to death is termed the critical thermal maximum temperature (Heatwole & Taylor 1987). For most species this temperature is below 45°C, although body temperatures of lizards measured in the field are usually substantially lower (Heatwole & Taylor 1987). Let us assume that body temperature equates to soil temperature and hence that lizards cannot be active when ground temperatures exceed 45°C. Note, however, that body temperature may be considerably higher than soil temperature because a lizard receives direct radiation as well as radiation from the soil surface. On the day when temperatures were measured (Figure 6.6), lizards would have had available only 2 h during which they could be active in sun-lit microhabitats compared with more than 6 h in shade. Hence shaded micro-habitats are likely to be very important for lizards throughout the warmer months of the year. In spring and autumn sites with low grazing levels had approximately 15% more shade compared to sites with high levels of grazing (Figure 6.5). In summer, when temperatures are higher and potentially more inhospitable, approximately 20% more of the ground is in shade at sites with low levels of grazing.

The percent of the ground in sun-light at different times of the day and year modelled separately for each site (Figure 6.7) highlights some distinct differences among replicate sites within each grazing level. Most notably, site L2 had substantially higher canopy cover than any of the other sites and plotted lowest on the graph (Figure 6.7). However, the shape of the curve for L2 suggests that the canopy may have been lower or less dense compared to the other sites, although horizontal cover was greater, because the rate at which the ground became progressively more shaded as sun angle decreased was lower. A higher degree of overlap between shade produced by individual trees may also partly account for the different shape of the curve compared to the other sites.

Shading from the tree canopy and from ground vegetation are both potentially important for lizards, and these variables are not necessarily independent. The relationship between canopy cover and the cover of ground vegetation at each site was examined to determine whether these features of the habitat were correlated at different times (Figure 6.8). In 1994 the cover of ground vegetation was low, and cover was
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Figure 6.6 Mean temperatures on sun-lit ground (triangles) and in the shade (squares) between sun-rise and sun-set on a clear spring day in mulga shrublands at the study sites. Maximum air temperature recorded at Alice Springs airport was 37°C. The dashed line indicates an approximate cut-off point (45°C), based on critical thermal maximum temperatures for lizards, above which soil temperatures are probably too hot for lizards to be active.
Figure 6.7 Differences between sites in the estimated percent of the ground in full sunlight at different times of the day and in different seasons showing differences between sites with high levels of grazing (open circles) and low levels of grazing (closed circles).
Figure 6.8 The relationship between canopy cover and cover of vegetation at ground level at each of the eight study sites in 1994 (open squares) and 1995 (closed triangles). There was a significant positive relationship between ground cover and canopy cover at site H2 in 1994 and at sites H1, H2, H3 and L1 in 1995 (see text).
similar among transects within each site. Vegetation at ground level was not correlated with canopy cover except at site H2 \( (r = 0.65, P = 0.002, df = 19) \). Cover increased in 1995 and, at several sites, the increase was higher at transects which had a high canopy cover (Figure 6.8). There was a positive correlation between canopy cover and ground vegetation at three of the sites with high grazing levels and one site with low levels of grazing \( (H1: r = 0.60, P = 0.005, H2: r = 0.65, P < 0.0001, H3: r = 0.63, P = 0.003, L1: r = 0.66, P = 0.002) \). At site L3, the site where the observed increase in the cover of ground vegetation was higher than at any other site (Figure 6.3), there was no relationship between canopy cover and ground cover in 1995, and this may reflect differences in the dominant species in the ground vegetation. The occurrence of ephemeral plant species, which are common in intergroves, may have been generally higher at sites with low levels of grazing.

**Relative abundance of lizards at different sites in a dry and wet year**

Lizard species captured in spring 1994 and 1995 are listed in Table 6.2. Fourteen species were captured at the study sites in 1994 compared to 20 in the following year. Geckos and pygopods were placed in a single group for the analyses presented in this chapter because all of the species captured were nocturnal and had a similar mode of foraging. The diurnal species were separated into skinks and agamids because the foraging modes of these families are distinctly different; agamids are sit-and-wait foragers whereas skinks are active foragers. Terrestrial, fossorial and arboreal species are included in the groups (Table 6.2) although the number of arboreal species and individuals were very few and make up a small part of each group. Different species within each group also have distinctly different food niches. However, the primary objective of assigning species to groups was to distinguish between species which were expected to respond differently to structural components of the vegetation based on their time of activity and foraging strategy, so I did not consider prey species when allocating species to groups.

There was no significant difference between the abundance of skinks at sites with different grazing levels in spring 1994, but in spring 1995 the number of skinks captured was higher in each of the sites with low levels of grazing \( (t_{tot} = 4.26, P = 0.005; Figure 6.9\ a) \). I have included data from autumn 1995 in the graph (Figure 6.9 a) to illustrate how relative abundance between sites changed during the two springs. In general abundance in autumn 1995, after the first drought breaking rains in December and January, was high compared to spring 1994. There was a slight decrease in abundance in the following spring (1995); however, at two of the sites with low levels of grazing, L3 and L4, the number of skinks captured continued to increase relative to before winter.
### Chapter 6: Relationships between vegetation cover, grazing and lizard abundance

Table 6.2 Lizard species captured during spring 1994 and 1995 and their primary temporal and spatial niches.

<table>
<thead>
<tr>
<th>Species</th>
<th>Time niche</th>
<th>Space niche</th>
<th>Captured in spring 1994</th>
<th>Captured in spring 1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>GEKKONIDAE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplodactylus ciliaris</td>
<td>nocturnal</td>
<td>arboreal +</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplodactylus conspicillatus</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diplodactylus stenodactylus</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Gehyra variegata</td>
<td>nocturnal</td>
<td>arboreal</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Heteronotia binoei</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Nephrurus levis</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Rhynchoedura ornata</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>PYGOPODIDAE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delma tintca</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Pygopus nigriceps</td>
<td>nocturnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>AGAMIDAE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenophorus nuchalis</td>
<td>diurnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lophognathus gilberti</td>
<td>diurnal</td>
<td>arboreal</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pogona vitticeps</td>
<td>diurnal</td>
<td>semi-arboreal</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>SCINCIDAE</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carlia munda</td>
<td>diurnal</td>
<td>terrestrial</td>
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<td>x</td>
</tr>
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<td>Cryptoblepharus plagiocephalus</td>
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<td>Ctenotus leonhardii</td>
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</tr>
<tr>
<td>Ctenotus schomburgkii</td>
<td>diurnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lerista desertorum</td>
<td>diurnal</td>
<td>fossorial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lerista labialis</td>
<td>diurnal</td>
<td>fossorial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lerista xanthura</td>
<td>diurnal</td>
<td>terrestrial</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Menetia greyii</td>
<td>diurnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Morethia ruficauda</td>
<td>diurnal</td>
<td>terrestrial</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

* These species are also recorded as being crepuscular and nocturnal

+ *Diplodactylus ciliaris* is also active on the ground in some habitats
Figure 6.9 The number of (a) skinks, (b) geckos and pygopods, and (c) agamids captured in spring 1994 (sp 94) and 1995 (sp 95) at each site. Sites with high levels of grazing are shown as open circles with solid lines, sites with low levels of grazing are shown as closed circles with dashed lines. Data for autumn 1995 (au 95) are also presented for skinks and agamids to show the relative abundance of these groups at an intermediate time between the two springs. For geckos and pygopods, summer (su 95) data are given for the same purpose, as captures in autumn 1995 were very low.
The number of skinks captured in spring 1995 at site L3 was much higher than in spring 1994. The increase in abundance of skinks was greater than at the other sites and corresponds with an equally dramatic change in the cover of ground vegetation at L3 over the period. Skink abundance at sites was compared with the cover of ground vegetation, separately in each year, to determine whether lizard captures varied consistently with the cover of ground vegetation at these times. The number of skinks captured was positively correlated with ground vegetation at sites in both years (spring 1994: $r^2 = 0.73, P = 0.007$; spring 1995: $r^2 = 0.54, P = 0.03$; Figure 6.10) even though abundance and ground cover differed considerably among sites and between these years.

An estimate of canopy cover for each site was derived from shade data as the percent of shade when the sun was 90° to the horizon. Skink abundance at site level was positively correlated with canopy cover in spring 1994 ($r^2 = 0.58, P = 0.03$) although this relationship was weaker than that between skink abundance and ground vegetation cover in this year. There was no significant relationship between canopy cover and skink abundance in 1995. Although there were few significant correlations between canopy cover and ground vegetation within sites in 1994 (Figure 6.8), among sites, canopy cover and ground vegetation cover were positively correlated in this year ($r^2 = 0.51, P = 0.04$). I used the residual deviations from the regression between ground vegetation and skink abundance in 1994 to test whether canopy cover was able to explain any of the variation in skink abundance in 1994 after the effect of ground cover had been removed. There was no significant correlation between canopy cover and the residual data for skink abundance ($r^2 = 0.08, P = 0.49$). If the abundance of skinks was directly affected by the cover of ground vegetation then this may also have resulted in a positive association between skink abundance and canopy cover because of the correlation between the two types of vegetation in this habitat during dry periods.

As a final exploration of this data I examined patterns of relative abundance of the two most abundant species of skinks, which gave considerable weight to the results presented so far, to determine whether the observed patterns in relative abundance at sites were consistent among different species or were largely driven by one particular species. Individually, neither species differed significantly in abundance at sites with different grazing levels in 1995 ($C. leonhardii$: $t_{df} = 0.82, P = 0.45$; $C. schomburgkii$: $t_{df} = 0.61, P = 0.56$). The relative abundance of all skink species differed greatly between sites (see also data presented in Chapter 2). For example, the abundance of $C. leonhardii$ at site L3 in spring 1995 was higher than at any other site, whereas few $C. schomburgkii$ were captured at this site. Both skinks were abundant at site L1 and
Figure 6.10 The relationship between the cover of ground vegetation at each of the study sites and the number of skinks captured in 1994 (squares) and 1995 (triangles). Symbols representing sites with high levels of grazing are open, and those for sites with low levels of grazing are closed.
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*C. schomburgkii* was also abundant at H4 at this time. Other skink species were locally abundant only at particular sites, *Morethia ruficauda* at L2 and *Lerista labialis* at L4 (Chapter 2). However, despite these variations among species, the relationship between abundance and the structure of the ground vegetation when all these species are considered together was consistent.

In contrast to skinks, the numbers of geckos and pygopods captured did not differ significantly between sites with different grazing levels in spring 1994 or spring 1995 (Figure 6.9b). In spring 1995 geckos were less abundant at all of the sites with high levels of grazing, except H4, compared to sites with low levels of grazing, but this trend was not significant (Figure 6.9b). The abundance of geckos at different sites varied considerably at different times, and there was no clear indication that the level of grazing at different sites can explain this variation.

Agamids were more abundant at three of the sites with high levels of grazing compared to lightly grazed sites in 1995 when the abundance of this group increased rapidly (Figure 6.9c). Clearly there was much variation between sites with high grazing levels; differences between sites with different grazing levels were not significant at any time, although the abundance of agamids was uniformly low at sites with low grazing levels.

The abundances of geckos and pygopods and of agamids were not correlated with vegetation structure, ground vegetation or canopy, in either of the two years.

**Discussion**

*Changes in vegetation cover and the abundance of skinks over time*

The results of this study support the hypothesis that the abundance of skinks, as a family group, is closely associated with the cover of ground vegetation at sites in mulga shrublands in central Australia. This relationship was consistent through time, but the relationship between the abundance of skinks and the level of grazing was not consistent. I propose that this is because vegetation cover differed considerably at different sites and over time, and sites with high levels of grazing did not always have lower cover than lightly grazed sites. My choice of sites in this study and definition of grazing level for sites were based on distance from water points provided for cattle, and there was considerable variation in vegetation cover between replicate sites within each defined level of grazing, both on the ground and at canopy level. Some of this variation may have been a result of differences in the history of grazing at each site or current stocking rates. However, underlying heterogeneity among sites, and variation
in rainfall at each site, also undoubtedly accounted for some of the variation, which was noticeable among sites at both high and low levels of grazing (Figures 6.3 & 6.8).

The change in cover of ground vegetation and the concurrent increase in the abundance of skinks at site L3 is noteworthy because it suggests that skinks responded rapidly to changes in the structural environment between years. In Chapter 3, I presented the results of an experiment to test whether differences in vegetation cover affect the rate at which lizards are captured in pitfall traps. No differences in rates of capture were found when lizards were confined in enclosures (Chapter 3), which indicates that the change in numbers of lizards captured in spring of 1994 and 1995 represents real differences between the abundance and activity of lizards at this time. Because no new hatchlings had appeared in the captured population in spring 1995 (Chapter 5) the increase in abundance of skinks at sites with low levels of grazing, and particularly at L3 and L4, relative to the other sites reflects either an increase in the level of activity of lizards at these sites or immigration from surrounding areas.

In mulga systems patterns of soil moisture are the primary factors influencing the distribution of plants. Groves of mulga occur in run-on areas which are generally favourable for plant growth and also support perennial grasses and shrubs, particularly along the margins (Ross & Lendon 1973). In contrast, there are few trees in intergroves, which are run-off zones, and these areas also support less dense stands of ground-level vegetation (Ross & Lendon 1973). Ephemeral species, however, are more common in intergrove areas and can be abundant after rains (Lendon & Ross 1978). Differences in the plant species comprising the dominant ground vegetation among sites, and their response to rainfall, may explain why the increase in abundance of skinks in 1995 differed in magnitude among individual sites. At sites with low levels of grazing, particularly L3, the cover of ground vegetation did not correlate with canopy cover in the second year, whereas in three of the heavily grazed sites canopy cover and ground cover were correlated. Hence, there may have generally been more ephemeral species at sites with low levels of grazing and a substantial increase in cover in intergroves in 1995 at these sites. This may have enabled skinks to disperse into intergroves which had previously provided few opportunities for shelter. I hypothesise that the increase in vegetation cover in 1995 enabled lizards at all sites to expand their range but particularly at sites where ground cover and canopy were not correlated and the diversity of shelter opportunities increased.

This explanation assumes that skinks responded primarily to ground vegetation, as the results indicate, but not to canopy cover. However, the amount of shade produced by the shrub canopy differed substantially between sites with different grazing levels, and the differences in temperatures between sun-lit and shaded microhabitats were
considerable. The distribution of thermal microhabitats in which a lizard can maintain its body temperature within viable limits is a major constraint on the activity of small lizards (Waldschmidt & Tracy 1983; Grant & Dunham 1988; Adolph 1990; Grant 1990). Even when activity is not restricted, the density of plants and the shelter they provide are likely to affect the body temperature of a lizard active within a habitat (Waldschmidt & Tracy 1983); body temperatures of active foraging lizards are often closely correlated with substrate temperature (e.g. Henle 1989b). Body temperature is a crucial factor for determining locomotory performance of lizards and hence their foraging efficiency and ability to escape from predators (Waldschmidt & Tracy 1983). Griffiths and Christian (1996) found that frill-necked lizards (*Chlamydosaurus kingii*) had different preferences for canopy cover in burnt and unburnt habitats and this may have been related to differences in thermal conditions or foraging strategies in these habitats.

Investigation of the use of thermal micro-habitats and body temperatures of lizards in mulga shrublands with different levels of grazing is beyond the scope of this study, but it is plausible that differences in the amount of shade produced by canopy cover among my sites affected activity levels of some lizards, and perhaps ultimately affected their abundance. Skink abundance was positively correlated with canopy cover, at site level, in spring 1994, but it is not clear whether this was a result of the correlation between canopy and ground cover. Because the number of lizards captured in each trap was very low, I was not able to analyse the distribution of lizards within each site with respect to vegetation structure. Pianka (1986) quantified the percentage utilisation of micro-habitats for a variety of lizard species in arid Australia, and among them were some of the species captured at my study sites. *Ctenotus leonhardii*, *C. schomburgkii* and *Menetia greyii* were most frequently found in Pianka's (1986) grass-sun, open-sun, and grass-shade habitats. Grass cover appears to be an important and frequently used micro-habitat for these species, whereas shade from canopy is not necessarily frequently used. So why do skinks respond to ground cover and not to canopy cover?

Vegetation at ground level also provides considerable shelter from extreme temperatures. In summer, temperatures under grass tussocks in the middle of the day are approximately 20°C cooler than the mean temperature on the ground surface (Hobbs & James *in press*). These temperature differences are similar to those between the sun and shade microhabitats which I have reported. Compared with shade from the canopy, the shelter provided by ground vegetation is more stable through time and space (it does not vary greatly at different sun angles) and hence may be a more reliable source of shelter for ground-active lizards. There is abundant evidence that reptiles respond to simple structural cues when they select micro-habitats (e.g. Sexton 1958; Sexton 1959; Heatwole 1966; Schlesinger & Shine 1994). In mulga shrublands,
ground vegetation may be the proximal cue to which diurnal skinks respond during their daily activity; by doing so they may automatically be exposed to a range of suitable thermal micro-climates. Temperature or light intensity are important cues for fine scale movement of lizards during their daily activity cycles but these factors may not be satisfactory cues for lizards to select suitable habitats, because they do not necessarily reflect long term average conditions (Heatwole 1977). In contrast, simple structural cues, such as the density of ground vegetation, may be consistently good indicators of habitat quality for skinks. As well as being exposed to a range of suitable thermal micro-environments, lizards that respond to these cues will also be sheltered from predators and may encounter increased abundance of some invertebrate prey.

I have not presented data for the abundance of prey species in this chapter; however, a brief discussion of the trends in invertebrate abundance during spring 1994 and 1995 is relevant here. Invertebrate biomass was considerably lower in spring 1994 than in spring 1995 (Chapter 4 & 5) and the scarcity of food resources almost certainly accounts, in part, for the delay in activity which resulted in few lizards being captured in spring 1994. However, the relative abundance of skinks among sites in spring 1995 cannot be attributed to the abundance of invertebrates. The total biomass of invertebrates that were sampled, excluding centipedes and scorpions which are too large to be prey species, was lower in all of the sites with low levels of grazing, except L3, in spring 1995 (unpublished data). This is the opposite trend to that for the activity of lizards, and also does not correspond with the body condition of lizards, a measure of mass in proportion to body length, at these times. Mean body condition of the two most abundant species of skink, _C. leonhardii_ and _C. schomburgkii_, was higher at sites with low levels of grazing in the third year of the study (Chapter 5); hence, the ability to acquire food resources was not necessarily related to the abundance of prey. Thus, although prey abundance may have been lower at sites with low levels of grazing in spring 1995, the abundance of skinks was higher and, at least for some species, individuals were in better condition. If lizards were able to expand their home range or increase their active time in response to an increase in ground cover, as I have proposed, it follows that their potential to acquire resources would also have increased. Hence, differences in body condition (Chapter 5) between sites with different grazing levels and through time may also be related, indirectly, to vegetation cover.

**Why do some lizard species not respond to the cover of ground vegetation?**

There were no significant correlations between the abundance of agamids and vegetation structure in spring 1994 or 1995, but the strong association of the most
abundant species, *Ctenophorus nuchalis*, with open areas (Heatwole 1970; Pianka 1971b) is the most likely explanation for the observed distribution and abundance of agamids at my sites. Nonetheless, the effect of differences in vegetation structure on thermal microhabitats, which has been a major focus of this chapter, may not be relevant for *C. nuchalis* because individuals of this species are tolerant of very high temperatures and are able to thermoregulate very precisely (Heatwole 1970). The foraging strategy of *C. nuchalis* is to sit and wait for passing prey, so individuals can choose perches which enable them to maintain preferred body temperatures and can thermoregulate precisely while foraging. This is in stark contrast to skinks which must be active on the ground during foraging activities and hence are directly exposed to a large range of temperatures within their home range. Additionally, compared with skinks, the larger body size of *C. nuchalis*, and the other agamid species I captured, results in greater thermal inertia and the ability to maintain body temperatures which differ considerably from environmental temperatures. Although I did not detect an inverse correlation between ground vegetation or canopy cover with agamids in spring 1994 or 1995, this may have been because the low numbers of agamids captured made patterns difficult to detect. The abundance of *C. nuchalis* pooled over 27 months of trapping was significantly correlated with the amount of bare ground at sites (Chapter 2). The high abundance of *C. nuchalis* in open areas is likely to relate to the foraging opportunities that these areas afford and is probably not related to differences in the thermal environment.

Most of the geckos captured at my sites, like agamids, forage in open areas (Pianka 1986), so why were geckos not more abundant at sites with high levels of grazing which were more open? Although vegetation structure may not have a significant effect on the availability of suitable thermal microhabitats for nocturnal species (Chapters 2 & 4), differences in ground cover may affect the foraging efficiency of geckos. I have not found any evidence to suggest this is so at my study sites (Chapter 5). I propose that, because ground vegetation in mulga shrublands is sparse, geckos probably do not experience a shortage of opportunities to forage on open ground, regardless of the grazing level at sites or of how much rain has fallen.

**Conclusions**

The significant differences between the abundance of skinks at sites with different levels of grazing in spring 1995 (this Chapter) and when data collected between September 1993 and December 1995 are pooled (see Chapter 2), suggest that the Scincidae are adversely affected by grazing in mulga shrublands. This pattern at family level reflects trends for individual skink species which may be partially
obscured by a combination of extreme temporal variation and spatial heterogeneity in abundance. These results need to be verified by further investigation.

The cover of ground vegetation is obviously only one of many factors contributing to the abundance of individual skink species across space and over time. Yet, as a family, the correlation between skink abundance and the cover of ground vegetation is an important result because it identifies a possible explanation for observed patterns of abundance of lizards at sites with different grazing levels. I propose that a combination of the life-history traits of skinks, primarily diurnal activity and active foraging, make this group more vulnerable to changes in vegetation cover associated with grazing in mulga shrublands compared to geckos, pygopods and agamids. The different responses of different lizard families to grazing in mulga shrublands has been discussed in previous chapters (Chapters 2, 4 & 5) and the results presented here are further evidence of distinct differences between families. These differences seem to reflect the responses of nocturnally and diurnally active species as well as species with different foraging modes.
Chapter 7

General discussion
GENERAL DISCUSSION

Temporal change in terrestrial lizard assemblages

The temporal patterns in lizard captures observed during this study reflect changes both in abundance and activity. For example, the progressive increase in captures of *Ctenophorus nuchalis* during the study appears to represent an increase in abundance, particularly because this species did not show clear fluctuations in the number of captures in response to environmental variables. However, many of the differences in the numbers of lizards captured over time can be attributed primarily to patterns of activity. For most species, with the exception of *C. nuchalis*, annual activity cycles which correspond broadly with changing temperatures are clearly evident (Chapter 4).

In addition to the effects of temperature on annual cycles of activity, lizards may become inactive for a number of other reasons. In the Australian arid zone, lizards can become dormant for long periods when conditions are harsh and the availability of food is low. Under these circumstances, although thermal conditions may be suitable for activity, there is no net energetic benefit from being active because the metabolic costs of activity exceed the energy gained from prey.

Even in months when activity levels are generally high, lizards may be inactive for short periods, lasting a few days, in response to daily weather conditions. Activity at body temperatures outside the optimal range affects sprint performance of lizards (Christian & Tracy 1981; Waldschmidt & Tracy 1983) and the ability to escape from predators is reduced (Whitford & Creusere 1977; Christian & Tracy 1981; Henle 1992). Hence, there is considerable advantage to being active only under thermal conditions which enable the attainment of body temperatures in the optimal range, and the number of hours when such conditions occur may vary considerably on different days (Chapter 6). Rose (1981) has proposed that voluntary inactivity for short periods even under favourable weather conditions may be an important adaptive strategy for lizards, provided energetic demands are met, because it decreases the risk of predation and conserves energy.

The optimal time for lizards to be active in the central Australian region would be when temperature conditions and prey abundance coincide to enable minimum energy expenditure to meet energetic and reproductive requirements and maximum avoidance of predators, but these conditions do not always coincide. Lizards must be flexible in their patterns of activity to take advantage of periods when the abundance of prey is high, and this may cause them to be active under sub-optimal thermal conditions. Alternatively, the activity of lizards during productive periods may be severely
restricted by the thermal environment. As I have suggested above (and see Chapter 4), lizards may become inactive in response to (1) annual cycles of temperature change, (2) lack of rain and scarcity of resources, (3) short-term weather fluctuations or, alternatively, (4) lizards may become voluntarily inactive under favourable conditions. I will briefly interpret the temporal patterns of activity of lizards observed during this study in the context of these factors and in relation to the prevailing climatic conditions in each year.

The spring of 1993 and spring 1995 were both relatively productive periods, and lizards became active early in the season, at a time which coincided with an increase in daily temperatures. Activity levels dropped off in autumn 1994 as the weather became cooler. Because resources were plentiful, lizards were able to be active during the warmest months of both years. Presumably many individuals were able to meet energetic requirements before winter temperatures restricted activity, and may have become dormant in autumn despite on-going favourable weather conditions. Within the peak period of activity in these years, thermal conditions were probably suitable for activity on most days. Voluntary inactivity, and to a lesser extent daily weather fluctuations, probably accounted for short periods when lizards were inactive.

In the driest period of the study, spring 1994, few lizards of any species were active (Chapter 4). Invertebrate biomass was also low, and for most species the body condition of individuals had reached low levels (Chapter 5). Environmental temperatures were similar to those during other periods when lizards were active, so the primary reason for being inactive in spring 1994 was probably the shortage of food resources. For diurnally active species, reduced ground cover, resulting from many months without rain, may have also limited opportunities to shelter from predators and from environmental extremes, especially on very hot days. Although invertebrate abundance and lizard abundance generally tracked each other throughout the study (Chapter 4), I found no evidence that lizard activity was correlated with invertebrate abundance over short time periods, neither did I find any correspondence between lizard and invertebrate abundance at different sites. The body condition of lizards also did not correspond closely to fluctuations in invertebrate abundance, except in the dry spring of 1994. I conclude, therefore, that spring 1994 was the only period during the study when the availability of food was the primary factor influencing the activity of lizards and affecting the physical condition of those lizards that were active.

Many lizards may not have been able to meet energetic demands by the end of autumn 1995 because of delayed activity and low prey abundance in spring 1994 and would have been advantaged by extending activity into the cooler months. Some lizards were active throughout 1995, which suggests that low winter temperatures did not restrict
activity entirely; however, winter activity would not have been possible, regardless of energetic demands, if temperatures had been similar to those in winter 1994 which was unusually cold. Even in the warmer winter of 1995, fluctuations in temperature within and among days would have been much more important for lizards than in summer, spring or autumn when average temperatures were higher. Some of the differences in the ways in which temperature and rainfall affect the activity of different lizard families were identified in the models presented in Chapter 4 (Figure 4.13). These differences are highlighted in the distinctly different patterns of activity of agamids, skinks and geckos in 1995.

Agamids were active throughout most of 1995, and both abundance and body condition of individuals increased during this period. Daily activity of *Ctenophorus nuchalis* did not correspond to daily fluctuations in temperature, probably because of a combination of the broad range of thermoregulatory behaviours exhibited by this species and the relatively warm winter temperatures in this year. *Ctenophorus nuchalis* seems to be less restricted by seasonal and daily temperatures than the other species captured (see Chapter 4; Figure 4.13 c), which enables individuals to respond opportunistically to productive periods, even when these occur in winter.

Skinks were also able to extend their activity into winter in 1995. The abundances of some species of skink were correlated with daily temperature in autumn and spring and there was a correlation between the abundance of skinks and the cover of ground vegetation at different sites; these relationships imply that the activity of lizards in this family is constrained by environmental temperatures to a greater degree than *C. nuchalis*. Presumably the interaction between environmental temperatures and habitat structure (Chapter 6) also affects the precision of thermoregulation these species can achieve, and thus may in turn affect their susceptibility to predation (Henle 1992; Waldschmidt & Tracy 1983). Nevertheless, the body condition of skinks increased during autumn and winter 1995, and the abundance of skinks in the following spring was relatively high, so extending activity (perhaps into periods when the thermal environment was sub-optimal) was almost certainly advantageous for this group.

Geckos did not extend their active period far into autumn and winter 1995. Compared with diurnally active species, the annual activity of geckos is closely locked into temperature cycles because temperatures are lower and opportunities for active thermoregulation are fewer at night (Chapter 4; Figure 4.13 b). Although geckos compensate, to some extent, by being active at lower and more variable body temperatures than diurnally active lizards (Huey *et al.* 1989), they are precluded from responding to peaks in productivity when these occur in cooler seasons. Consequently, unlike for skinks and agamids, the body condition of geckos did not
increase during 1995. However, the body condition of geckos, unlike the other species groups, was not unusually low in the previous spring. These results imply that, although geckos were not able to benefit from the productive period in autumn 1995, they were less affected by the combination of low invertebrate abundance and reduced ground cover which seemed to result in low activity and body condition of skinks in spring 1994.

Geckos, as nocturnally active lizards, may be less affected by periods of drought than skinks because:
(1) nocturnally active prey, in particular termites, may be more abundant during drought compared with prey which are active during the day (e.g. see James 1991d);
(2) the metabolic costs of activity during periods when prey resources are limited may be less for nocturnal lizards because they are active at lower body temperatures; and,
(3) reduced cover of ground vegetation associated with drought is less likely to directly limit the activity of nocturnally active lizards, or their prey, because the thermal environment at night is less dependant on vegetation structure than during the day.

I emphasise that nocturnal and diurnal activity, rather than taxonomic differences, may be the key to understanding the responses of geckos and skinks to the climatic conditions which I observed during this study. Even within a single genus, nocturnal activity may confer advantages to some species under some circumstances. For example, James (1991a) found that in a dry year the skink *Ctenotus pantherinus* was reproductively active whereas other sympatric species of *Ctenotus* were not and that the body condition of *C. pantherinus* was also higher than that of the other species at that time (James 1991c); *Ctenotus pantherinus* was the only species which was recorded as being active at night.

Flexibility and opportunism in response to variable rainfall and food resources are fundamental strategies for survival in the deserts of central Australia, and the ways by which vertebrate animals achieve these are as many and varied as the species which occur in the region. For lizards, response to highly productive periods can only occur within the constraints of the thermal environment, and the degree to which environmental temperatures constrain activity differs widely among species. Equally, temperature may be more important in determining short-term patterns of activity when energetic demands cause lizards to be active in sub-optimal thermal conditions. This study has identified distinct differences between diurnally and nocturnally active lizard species in their patterns of activity and their response to changes in resource availability over time as measured by growth and body condition. Ultimately, the differences among species which cause these disparate responses may also affect the susceptibility of each species to changes brought about by grazing.
The effect of grazing around water points on lizard assemblages

Low metabolic rates, an ability to survive without food or water for long periods, and the ability to enter a dormant state when prey abundance is low are all attributes which enable lizards to be highly successful in arid environments. These same attributes may have resulted in lizards being relatively insensitive to reduced levels of primary production which can result from grazing. No Australian desert-dwelling reptile is known to have become extinct since Europeans settled in Australia (Ehmann & Cogger 1985) and populations of individual species appear to have persisted in high numbers. In comparison, the mammals of inland Australia have experienced numerous extinctions and contractions in range (Morton 1990). Nonetheless, evidence is slowly emerging that reptiles, like other vertebrate groups, have not escaped from the impact of grazing. I have found that lizard assemblages in mulga shrublands differed between sites with different grazing levels in the abundance of individual species and of family groups.

With the exception of Heteronotia binoei, I found no evidence that any of the nocturnally active species captured during this study, which included geckos and pygopods, differed in abundance between sites with different levels of grazing. I have, however, found that diurnally active species differed in abundance at sites with high and low levels of grazing. The agamid Ctenophorus nuchalis was captured almost exclusively at heavily grazed sites, close to a water point. In contrast, skinks were significantly more abundant at sites which were far from a water point, and thus lightly grazed, reflecting a consistent trend among the majority of species within this family. The abundance of skinks was positively correlated with the cover of ground vegetation, although the relative cover of vegetation at sites with different levels of grazing varied over time. The effect of grazing on vegetation cover seems to be the mechanism by which grazing affects the abundance and activity of skinks. The interactions between grazing, vegetation cover, and rainfall explain why differences in the abundance of skinks between sites with different levels of grazing were only detectable at some times.

In my discussion of the dry spring in 1994 I identified two factors which I believe primarily explain the low rates of capture and low body condition of many lizards at this time; low prey abundance and reduced cover of ground vegetation. I did not find any significant differences in invertebrate biomass between sites with different grazing levels but, because I did not collect data specifically relating to prey species, more data are required to determine with certainty that the availability of prey did not differ according to the level of grazing for some species. Any undetected changes in prey abundance resulting from grazing may be less severe for nocturnal lizards if the costs
of prolonging activity to acquire more resources are lower than for diurnal lizards. Grazing, like a long period without rain, reduces the cover of ground vegetation, at least under some conditions. The effect of a reduction in ground cover on the thermal environment, irrespective of whether grazing or drought is the mechanism, is not likely to be important for nocturnal lizards; however, for diurnal lizards the thermal environment during the active period may be substantially changed. Diurnal and nocturnal lizards respond differently to periods of low productivity and plant cover, as I have discussed throughout this thesis. Nocturnal lizards may be less severely affected by drought, but the potential for diurnally active lizards to recover during highly productive periods may be greater. Both strategies have obviously been highly successful over evolutionary time, but the differences between them may mean that nocturnally active lizards are better equipped to deal with environmental changes brought about by grazing.

Future work and recommendations

The results of my study highlight the complexities of the dynamics of lizard communities in highly variable environments which are also subject to environmental impacts. More information about the effect of grazing on lizard communities under other climatic sequences is required, as this study encompasses only a sample of the climatic variability which characterises this environment.

I recommend that future studies should carefully consider the timing of survey and preferably encompass a range of climatic conditions. In many situations, however, it is not logistically possible to sample for long periods. In this case preference should be given to sampling for shorter periods over a number of years, rather than over several seasons, so that data for years with different rainfall are available. Annual sampling should take place when populations are expected to be high enough to enable detection of differences between sites where these exist. The temporal patterns of activity observed in this study suggest that, in arid Australian mulga lands, lizards are only active in high numbers in spring when there has been rain in the preceding winter and spring. The use of a simple model to predict herbage growth from rainfall data would enable distinction between small rain events and more significant rainfall which leads to substantial plant growth to which invertebrates and lizards are likely to respond (see Chapter 4). Lizards may be particularly active in autumn when a dry spring is followed by summer or autumn rain. Summer, however, is the best time to sample for a study which spans several years because temperatures will be high, and many lizards will be active, regardless of whether activity commences early in spring or is delayed on account of low rainfall. If shorter studies in one year only must be undertaken, the decision about when to sample should be made by considering rainfall conditions and plant growth models.
The distinction between nocturnal and diurnal lizards in their response to variable rainfall and in their abundance at sites with different levels of grazing offers a broad framework for future studies.

(1) Are nocturnal lizards less affected by periods of drought in terms of their abundance and reproductive success than diurnal lizards?
(2) Are nocturnal lizards less affected by grazing than diurnally active species?
(3) Is the response of different species to the cover of ground vegetation the key to understanding differences between nocturnal and diurnal species in their response to drought and to grazing?

Another question is whether the relationships that I have demonstrated between the abundance of diurnal lizards (particularly skinks) and vegetation cover are consistent over longer periods of time, and in other habitats? To answer this, a study specifically focussing on the relationship between the abundance of lizards and vegetation cover is required. Sampling should seek to separate the effects of grazing and vegetation cover to determine definitively whether change in ground cover is the mechanism by which grazing affects some lizard species. The study also needs to be undertaken for an adequate period to ensure that a variety of rainfall conditions are encountered, and must have appropriate measurements of ground cover at all sites and times, to determine whether relationships between vegetation cover and lizard abundance are stable through time. When the relationships between lizard abundance and vegetation cover are better understood, it will be possible to predict the effects of grazing on lizards over large areas, based on pre-existing data for plant cover.

The relationship between the cover of ground vegetation and the abundance of skinks also requires specific investigation at finer scales. For example, information about the thermoregulatory behaviour and body temperatures of ground active skinks in areas with different vegetation cover, at ground and canopy level, will determine whether vegetation cover affects the thermoregulatory opportunities available to these lizards. The suitability of the structural configuration of the habitat for a particular mode of foraging may be as important as the thermal properties of a habitat in determining the abundance and activity of some species. Detailed study of the behaviour of skinks under different rainfall conditions which result in changes to the cover of ground vegetation would also be useful. Do daily activity times differ for diurnal species according to vegetation structure? Do lizards extend their home ranges when alternative cover is available? Manipulative experiments in which additional cover is provided for lizards, simulating the result of a rainfall event, would be useful for teasing out the specific ways by which lizards respond to a variable physical environment.
Research in the areas I have outlined, as well as continued research on the effects of grazing on a range of biota on a regional scale (see Landsberg et al. 1997), is highly desirable. Additionally, active management is required now so that areas which have had relatively little disturbance are preserved. These areas will be crucial in enabling the testing of predictions of the effect of grazing on native animal communities in the future. Grazing by cattle has resulted in considerable change to habitats in the central Australian region. This study has shown that variations in ground cover which result from concentrated grazing around artificial water points affect the abundance of some lizard species. Based on these findings, I recommend that the current diversity of habitats be maintained until further information is available on the long term effects of grazing, particularly for vulnerable species, and that the installation of new water points in areas which are currently remote from water should be avoided where possible.
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